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THE
BOTANICAL GAZETTE

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THE CAUSES OF VEGETATIVE CYCLES[1]

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HENRY C. COWLES

1. The demonstration of vegetative cycles

The work of the past decade has shown most clearly that there are cycles of vegetation, which are comparable precisely to cycles of erosion; in each there is a period of youth, which is characterized by vigor of development and by rapidity of change; in each there is a period of maturity, and finally one of old age, which is characterized by slowness of transformation and by approach to stability, or at least to equilibrium. At the close of the vegetative cycle there is no such universal feature as the base level of the physiographer, since the final vegetative aspect varies with the climate, and hence is called a climatic formation. In the eastern United States, the final stage is a mesophytic deciduous forest; farther to the north and in the Pacific states, it is a coniferous forest; in the great belt from Texas to Saskatchewan, the final stage is a prairie; and in the arid southwest, it is a desert. In every case, the ultimate or climatic plant formation is the most mesophytic which the climate is able to support in the region taken as a whole. In a prairie climate there may be trees, but they occur for the most part near lakes or streams, or in protected depressions, and in the base-leveling of the region they give way to the prairie; quite the same may be said of trees in a desert climate.

It has been ascertained that the original plant formations in any habitat give way in a somewhat definite fashion to those that come

[1] Address delivered as retiring president of the Association of American Geographers, Pittsburgh, December 29, 1910.

after. Pioneer formations usually are hydrophytic or xerophytic, mostly xerophytic in arid climates, and more equally divided in moist climates. For example, the last retreat of the glacial ice left in our northern states a vast tract made up essentially of hills and hollows, the hollows, if deep enough, with lakes. The first vegetation of the hills was xerophytic, and the first vegetation of the hollows, hydrophytic. Finally, except on the higher hills and in the deeper hollows, these first plant formations gave way step by step to the climatic tundra, and, as the climate became ameliorated, this in turn gave way to climatic coniferous forests, and then to climatic deciduous forests as they exist today. So far have the higher hills and the deeper hollows lagged behind the less extreme habitats in their development that there are still to be found many places which continue to have pioneer formations, though, of course, they differ greatly from the original pioneer formations of the tundra.

While the general trend of vegetation is from diversity toward uniformity, it must not be supposed that complete similitude is ever reached even under like climatic conditions. There are species, for example, in the culminating forest of New England which do not occur in Ohio, and species in Ohio which do not occur in Illinois; southward the difference is even more pronounced. And yet it cannot be denied that from the Maritime Provinces to Minnesota and south to the coastal plain the ultimate forest in its larger features is of a single type; the percentages and even the kinds of dominating trees may differ, but the aspect is essentially the same. Much more diverse from one another than are the beginnings or the ends are the intervening stages. Our northern lakes, for example, differ much less from one another in their floristic composition than do the swamps to which they give rise. The initial stages of a rock upland in Tennessee and in northern Michigan are much alike, both in aspect and in floristic composition; the terminal stages in these two widely separated districts are even more alike, but the intermediate stages are very different, northern Michigan having nothing at all comparable to the oak stages in the vegetational development of eastern Tennessee, and the latter region being without the complex coniferous stages of northern Michigan.

In this instance it is likely that some of the northern coniferous stages correspond to some of the southern oak stages; thus we may speak of *alternative* or *substitute* stages, when different plant formations occupy equivalent places in a successional series.

In a desert climate an upland may exhibit almost no succession, since the original xerophytic formation may remain with but little change; in comparison with a successional series in a mesophytic climate, one may speak here of the *elimination* of certain stages. In marked contrast to the lack of succession or to the slow succession on a desert upland is the rapid succession on uplands in humid climates; indeed, it is possible here for mesophytes to exist side by side with xerophytes in the pioneer stages—in such a case one may speak of *telescoped* successions. Even in a climate like that of the eastern United States, telescoping may take place, as in the successions of rich fallow land and in those which follow the cutting of a mesophytic forest. With this brief survey of recent progress in the field of physiographic ecology, we may pass to a similarly brief consideration of the historical development of vegetative dynamics, and then to a consideration of the main theme of the address.

2. The development of dynamic plant geography

The systematic exploitation of developmental or dynamic plant geography presupposes the establishment of the principles of dynamic geology and of organic evolution; hence it could not have antedated LYELL, who brought general recognition of the former, or DARWIN, who brought general recognition of the latter. Results frequently lag far behind their causes, and it is only now, a full half-century after the publication of DARWIN'S *Origin of species*, and three-quarters of a century after the appearance of LYELL'S *Principles*, that the dynamic method is coming to be regarded as the most fundamental thing in plant geography. As in other branches of science, there have been prophets far in advance of their time, though it is only within the last decade that the prophetic insight of these pioneers has had recognition. LYELL records the struggle of the developmental idea in geology, as opposed to the ruling theories of special creation or catastrophism, noting especially the keen philosophy of certain ancient Greeks

and the renascence of these views in Italy through the influence of LEONARDO DA VINCI and of other great contemporaries and followers.

So far as we know, the beginnings of dynamic plant geography are much more recent than are the beginnings of dynamic geology, nor is this strange, since it is easier to recognize the destruction of land by waves and the deposition of material by rivers than to observe the more silent transformation of one plant association into another. Doubtless the earliest observers of such transformations failed to record the things they saw. It is hardly to be doubted, for example, that long ago many a philosophic woodsman must have noted, when he cut down the trees of a forest, that there sprang up a new vegetation differing from the old, and that gradually these first trees of the newly developing forest were displaced by other trees; and there may have been some who were keen enough to see that, after a long time, there was a return to the primeval type of forest.

The earliest account which I have discovered that clearly deals with vegetative dynamics is in a short paper in the *Philosophical transactions* in 1685, in which WILLIAM KING (1) gives a good account of the origin of bog vegetation from floating mats; many times since, this has been reported as an original discovery. Perhaps the first to have a real glimmer of the doctrine of succession, as understood today, was the great French naturalist BUFFON. Although better known for his splendid descriptions of animals, BUFFON in his earlier life was much interested in forestry, and in 1742 he noted (2) that poplars precede oaks and beeches in the natural development of a forest. As a result of this observation, he gave the important advice to foresters that if they wished to cultivate beeches, they should plant them not in the open, but in the shade of those trees which they naturally succeeded. BIBERG (3), a student of the great LINNAEUS, published his thesis in 1749, and in this he describes the gradual development of vegetation on bare rocks; here he observes accurately the pioneer activity of the lichens and mosses, and he notes as well the importance of *Sphagnum* in the development of bogs.

The seeds planted by BUFFON and BIBERG fell on sterile soil; in

France it was observed that BUFFON was trespassing on theological grounds, and he was obliged to recant any views which implied that the world was not made in the beginning once for all; in Sweden the influence of LINNAEUS was wholly against anything dynamic; he never published anything dynamic himself, and when a student like BIBERG set his face in that direction, the master frowned, and said that the student was departing from the true mission of the botanist. It is not strange, therefore, that there followed a sterile period of three-quarters of a century. Yet it was within this period that plant geography was first recognized as a definite branch of science, for this was the period of HUMBOLDT. This also was the period of JOACHIM SCHOUW, who published the first general plant geography, and of the older DECANDOLLE, who gave the weight of his great name to several important treatises in the new subject. But none of these men, not even HUMBOLDT, were permeated with the dynamic principle, so far at least as plant geography is concerned. They placed descriptive plant geography on a solid foundation, and gave it such momentum that for a full century it dominated the entire field of plant geography; indeed in certain places it dominates plant geography today.

France, so often the birthplace of great ideas, gave the pendulum an impulse in the right direction. The sane influence of BUFFON had not altogether been suppressed by the theologians, and finally there arose such men as JUSSIEU, who introduced a flexible natural system of plant classification, which finally displaced the rigid artificial system of LINNAEUS, thus making possible the development of evolutionary theories; such men as LAPLACE, who conceived a theory of planetary evolution, thus making possible the development of evolutionary theories in other lines of science; and such men as LAMARCK and GEOFFROY STE. HILAIRE, who propounded evolutionary theories in biology. The birth of dynamical conceptions in France a century ago rejuvenated science throughout Europe, making possible the development of a LYELL and a DARWIN. It also made possible the development of a dynamic trend in the new science of plant geography, though, as previously noted, the momentum given to descriptive geography was too great readily to be overcome.

Very properly the first work of the new period along dynamic lines was done in France; in 1825 DUREAU DE LA MALLE (**4**) published the first paper which gave the results of a careful study of plant succession involving the observations of a number of years. His work was done mainly in cut-over areas of forest, and no work done since greatly surpasses it in accuracy and thoroughness. The marvelous clear-sightedness of DUREAU DE LA MALLE is well shown in the title of his chief contribution, which (in English rendering) is: "Memoir on alternation or on alternative succession in the reproduction of plant species living in association (*société*)—is it a general law of nature?" DUREAU DE LA MALLE (not STEENSTRUP, as frequently supposed) first used the term succession in the present sense; probably he was the first also to use the term society as an expression of plant grouping. The year 1845 is a noteworthy one because it was then that EDWARD FORBES gave a short paper (**6**) before the British Association, opening up an entirely new line of study, namely, the interpretation of past geographic features by the present. He was the first to understand the significance of endemism in relation to previous connections between islands and continents that now are isolated.

In 1841 a great advance was made by the Danish geologist STEENSTRUP (**5**), who discovered the possibility of using the fossils of the immediate (i.e., postglacial) past as a means of interpreting the climatic changes and the correlated vegetation changes of recent epochs. VAUPELL, a student of STEENSTRUP, but more botanically inclined, applied his ideas in detail (**7, 9**), and in the years between 1851 and 1863 gave to the world his famous account of the postglacial development of Danish vegetation, showing that the birch was the chief early pioneer, and that later it was followed in turn by the pine and the oak, and finally by the beech, which dominates today. From 1856 to 1859 REISSEK (**8**) worked out the dynamical development of the vegetation on the islands of the Danube. In 1876 GREMBLICH (**10**) seemed to realize the actuality of cycles of vegetation. In 1881 HULT, a Finnish botanist, made the first comprehensive study of succession (**11**) as it is now taking place in a given region, and he was the first to recognize that a comparatively large number of pioneer plant associations later

give way to a comparatively small number of relatively permanent associations.

In 1888 TREUB, whose recent premature decease we so keenly regret, began the study of the new vegetation of Krakatoa (**12**), thus inaugurating one of the most fruitful lines of investigation in dynamic plant geography. In 1891 WARMING, to whom more than to any other we owe the present large place occupied by ecological plant geography, published the first of his developmental studies of Danish dune vegetation (**13**). This was followed by a similar treatment of the Rhône delta by FLAHAULT and COMBRES (**14**), and of the North German heath by GRAEBNER (**16**), and also by WARMING'S *Plantesamfund* (**15**), the original Danish edition of his well known *Plant geography*, in which there is much material of dynamic import, together with the formulation of a number of "laws of succession." In 1896 MEIGEN (**17**) made a systematic study of succession, somewhat along the lines previously followed by HULT, and he showed that there is a final tendency toward equilibrium. This brings us to the period in which dynamic plant geography was taken up actively in this country, and here our historical résumé may well give place to the main topic of this paper.

3. The delimitation of successional factors

No systematic attempt has been made hitherto to group in an analytic manner the phenomena of succession from the standpoint of their causation. WARMING (**15**) made a great advance toward this end by gathering together the known records of vegetative change or succession; he noted that vegetative change is particularly evident on new soil (as along sandy shores, and in marshes, on lava, on landslip soil and talus, and on burned and fallow land). He summarizes his studies by giving six laws appertaining to succession. CLEMENTS (**21**) attempted to distinguish between primary and secondary successions, the former being those on newly formed soils, and the latter those on denuded soils. This classification seems not to be of fundamental value, since it separates such closely related phenomena as those of erosion and deposition, and places together such unlike things as human agencies and the subsidence of land. CLEMENTS, like WARMING, gives a summary of results in the form of laws.

While most observers very properly have paid chief attention to the actual facts of succession rather than to their underlying causes, a scrutiny of past results shows very clearly that the phenomena considered have differed greatly in kind. Obviously the phenomena of bog development, as observed by WILLIAM KING, had to do with a succession in which the activities of the plants themselves played the leading part; the humus accretions of the bog plants, such as the peat moss *Sphagnum*, made possible the development of another vegetation on a higher soil level. In a comparable manner, the successions observed by BUFFON, by BIBERG, and by DUREAU DE LA MALLE had to do with plant activities; the forest trees of a given generation cast the shade necessary for the development of other trees which need shade rather than light for their development; BIBERG'S lichens accumulated a soil which made possible the development of higher vegetation on rock surfaces. STEENSTRUP, however, in his study of the fossils, introduced to the scientific world a new kind of succession phenomena, for in his elucidation of the postglacial history of Denmark there were recorded changes of broader significance than those hitherto observed; it was clear that the transition from the tundra vegetation through the birch and pine vegetation to the oak and beech, as developed by him and by his student VAUPELL, was a record of climatic change, inasmuch as the very same horizontal succession may be observed today in journeying from northern Scandinavia to Denmark. A third and equally diverse kind of succession phenomena was recorded by REISSEK in his study of the islands in the Danube, for here there was clearly recognized the influence of physiographic change on vegetation. Thus in succession we may distinguish the influence of physiographic and of biotic agencies. The physiographic agencies have two aspects, namely, regional (chiefly climatic) and topographic.

4. Regional successions

Regional successions are so slow in their development that they can be studied almost alone by the use of fossils. Hence the experimental method, which has proven so potent in unraveling many a biological tangle, is here of no avail. It is not strange, therefore,

that these successions are and probably must remain the least understood of all. There are, perhaps, four great examples of extensive regional change, which may be accepted as demonstrated, namely: (1) the change from the Carboniferous to the Permian, which is made evident particularly through the replacement of the carboniferous ferns, fern allies, and primitive gymnosperms by the *Glossopteris* flora and later by the modern gymnosperms; (2) the subordination of the gymnosperms to the angiosperms in the Cretaceous; (3) the elimination of tropical forms in boreal regions in the late Tertiary; and (4) the postglacial invasion of southern forms into boreal regions accompanying and following the retreat of the glacial ice. Generally it is held that the dominating factor in these vegetative successions is climatic change, and that this climatic change is chiefly one of temperature. Of this there can be no doubt in the case of the changes immediately before and after the Pleistocene ice invasion. The constant relation between glaciation and the development of the *Glossopteris* flora in the Permian makes it likely that the general vegetative changes of that epoch also were due primarily to temperature.

On the whole, however, there has been a general tendency to overestimate the influence of temperature as an ecological factor. The trend of nearly all experiment has been to show that water is of vastly greater importance, and it well may be that the change from the atmospheric humidity which seems to have characterized the Carboniferous to the aridity which seems to have characterized the Permian had more to do than did the decreased Permian temperatures with the elimination of the carboniferous flora and with its replacement by mesozoic forms. The most puzzling of the great vegetative transformations of the past was the sudden change from the dominantly gymnospermous forests of the Jurassic to the domination of the world by angiosperms in the Cretaceous. We know that after the Permian there was a gradual climatic amelioration toward genial conditions similar to those which characterized the Carboniferous; this amelioration seems to have culminated in the Cretaceous, which, like the Carboniferous, was also a period of extensive base-leveling. Very probably the high temperatures and the great atmospheric humidity of the Cretaceous gave con-

ditions that particularly favored the angiosperms, which as a group are much more mesophytic than are the gymnosperms.

To summarize on regional successions, it would seem that secular changes in climate, that is, changes which are too slow to be attested in a human lifetime, and which, perhaps, are too slow to be attested in a dozen or a hundred lifetimes, are the dominating factors. It is possible that these changes sometimes are more rapid than at other times, and there are those who would have us believe that the climate now is growing warmer, as witness the rapid recession of many of our North American glaciers; there are others who are quite as sure that the climate is growing colder, as witness the southward retreat of the "timber line" in Scandinavia. Still others feel equally confident that the recession of glaciers is due to increasing aridity; this explanation has the advantage also of accounting for retreating "timber lines." And there yet remain some who believe that all such changes may be of short duration, as it were cycles within cycles, or feeble and short-lived oscillations of great climatic waves. It is to be pointed out that great earth movements, either of elevation or subsidence, that is, the far-reaching and long-enduring epeirogenic movements, as contrasted with the oscillations of coast lines, must be considered in accounting for regional successions; the elevation of the Permian and the base-leveling of the Cretaceous must have played a stupendous part in instituting vegetative change.

5. Topographic successions

In striking contrast to secular successions, which move so slowly that we are in doubt even as to their present trend, are those successions which are associated with the topographic changes which result from the activities of such agents as running water, wind, ice, gravity, and vulcanism. In general these agencies occasion erosion and deposition, which necessarily must have a profound influence upon vegetation. I have considered in another place and in some detail (**18, 19, 20**) the influence of most of these agencies, and it will suffice in this place to summarize a few of the leading kinds of phenomena that are involved. As might be expected, the influence of erosion generally is destructive to vege-

tation, or at least retrogressive (i.e., tending to cause departure from the mesophytic), while the influence of deposition is constructive or progressive (i.e., tending to cause an approach toward the mesophytic). Progressive successions are well illustrated in the development of flood plains along rivers, and in the growth of sandy shores; retrogressive successions are associated with the eroding activities of streams and of receding shores.

Sometimes erosion may not have a retrogressive influence and sometimes the effect of deposition is not progressive. For example, on a somewhat rapidly eroding clay cliff of Lake Michigan, there often occur certain xerophytic annuals, which develop during the comparatively stable summer period, and a few perennials, such as the sumac and *Equisetum*, which have underground organs that enable them to migrate landward as fast as the cliff recedes; here we have a remarkable instance of rapid topographic change without a corresponding plant succession, either progressive or retrogressive. A marked increase in erosive intensity would destroy all vegetation, and a marked decrease in erosive intensity might institute a progressive vegetative succession. Deposition unaccompanied by progressive changes may be illustrated by an instance from the Lake Michigan sand dunes. Frequently a growing dune is inhabited by xerophytic annuals and by a few shrubs or trees (as various willows and the cottonwood); such a place illustrates the extreme of topographic dynamics, but often the vegetation is static. A great increase in depositional intensity results in the destruction of all the plants, while a decrease in depositional intensity results in progressive succession. Retrogression or a static condition of vegetation is to be seen also along rapid streams, where there is a considerable deposition of coarse material. A striking illustration of retrogression associated with deposition is afforded by lava flows.

6. Biotic successions

A. GENERAL FEATURES

Of less interest, perhaps, to the physiographer than are the vegetative changes hitherto considered, but of far greater import to the plant geographer, are the vegetative changes that are due to

plant and animal agencies. These are found to have an influence that is more diversified than is the case with the physiographic agencies; furthermore, their influence can be more exactly studied, since they are somewhat readily amenable to experimental control, but particularly because they operate with sufficient rapidity to be investigated with some exactness within the range of an ordinary lifetime. If, in their operation, regional agencies are matters of eons, and topographic agencies matters of centuries, biotic agencies may be expressed in terms of decades.

It has been seen that changes of climate or of topography generally institute vegetative changes; indeed this would have been predicted to be the case, even without examination. But at first thought it seems somewhat striking that far-reaching vegetative changes take place without any obvious climatic change and without any marked activity on the part of the ordinary erosive factors. Indeed, it is probably true that the character of the present vegetative covering of the earth is due far more to the influence of these relatively silent and subtle factors than to the more obvious factors previously considered. So rapid is the action of the biotic factors that not only the climate, but even the topography may be regarded as static over large areas for a considerable length of time. It has been said that many of our Pleistocene deposits exhibit almost the identical form which characterized them at the time of their deposition; in other words, the influence of thousands of years of weathering has been insufficient to cause them to lose their original appearance. These thousands of years would have sufficed for dozens and perhaps for hundreds of biotic vegetative cycles. Many a sand dune on the shores of Lake Michigan is clothed with the culminating mesophytic forest of the eastern United States, and yet the sand dunes are products of the present epoch; furthermore, sand is regarded generally as a poor type of soil in which to observe rapid succession. If a clay upland were denuded of its forest and its humus, it is believed that only a few centuries would suffice for the mesophytic forest to return.

From the standpoint of dynamic plant geography our land areas are divided into two well marked categories: on the one hand is the erosion topography that is characteristic of the eroding and

depositing phases of present streams and shores, and on the other hand is the *pre-erosion* topography (as it may be termed) which is characteristic of those areas that have not as yet been invaded by erosive forces. In our northern states the areas characterized by the presence of a pre-erosion topography often greatly exceed in extent the areas which are characterized by an erosion topography. South of the glaciated region, however, the areas characterized by the presence of an erosion topography often greatly dominate. But the influence of biotic agencies is not confined to areas that are characterized by a pre-erosion topography. For example, in our eastern forested region the development of a ravine, which furnishes a characteristic illustration of rapid topographic dynamics, exhibits only here and there actual erosion or deposition; the ravine slopes as a whole are covered with a mesophytic vegetation, because at a given spot the interval between periods of active erosion often is sufficiently long to permit the development of an entire biotic cycle. Perhaps in no other way could there be brought out more strikingly the durational contrast between topographic and vegetative cycles; a ravine is an index of extreme topographic youth, and yet in its development there is ample time for the complete development of many vegetative cycles. Quite as in ravines, the cliffs of streams and shores often exhibit temporary exemption from erosion, whereupon there is at once instituted a biotic cycle, which often has sufficient time for complete development before erosion again becomes active.

B. THE HUMUS COMPLEX

a. Water.—It is now time to consider the varying aspects of the biotic agencies which institute succession. Of these the first to be mentioned, because of its unquestioned supremacy, is the accumulation of humus. There are a number of different ways in which the accumulation of humus affects the trend of succession. It can scarcely be doubted that the most important of these humus influences, and perhaps the most important of all influences, inheres in the change which the humus brings about in the water relation of the soil. Speaking generally, humus accumulation occasions an increase in soil moisture on uplands and a decrease in

soil moisture in depressions; hence it is probable that the changed water relation due to humus accumulation is the dominating factor in determining the mesophytic trend, both in hydrophytic and in xerophytic habitats. Although bare sand supports a xerophytic flora, the accumulation of a thin humus layer is sufficient for forest development, and the Michigan dunes show that the most mesophytic of our forests can grow on a sand dune, if there is present a humus layer a few centimeters in thickness. On rock uplands, lichens commonly are the first humus accumulators; not only do they contribute humus by their own decay, but they give shelter and anchorage to plants of higher order, whose humus-accumulating capacity is greater. As long as the vegetation is open, and the humus exposed to the sun and wind, accumulation is slow, because of oxidation. But when the vegetation cover is more fully developed, the humus is more and more protected and hence accumulates more rapidly.

The relation of swamp successions to humus accumulation is particularly close. For each level both below and above the water table, there is a characteristic plant formation. In the deeper ponds only submersed aquatics can develop, but after a time their humus débris accumulates to such an extent that plants with long stems or leaf-stalks (such as the pondweeds and water lilies) are able to develop. They in turn build up the humus and prepare the way for their own elimination and for the development of such plants as the bulrush, which grows in shallow water. The latter again prepare the way by further humus accumulation for the first land plants, and they again for others. In all this well known successional series, the dominating factor clearly is a decreasing water content due to the accumulation of humus.

b. Soil organisms.—Another important influence associated with humus accumulation is the increase of soil organisms. These may play a part scarcely second to water, but as yet we know all too little of their activities to be certain of their precise place in the scale of importance. We know, however, that nitrogen is one of the essential plant constituents, and that it is made available chiefly by certain bacteria and fungi. Since these forms live on decaying organic matter, it seems likely that humus accumulation

is likely to favor their increasing development and hence an increasing supply of available nitrogen. A single instance will suffice to show the possible importance of soil organisms in succession. The beech, which is a characteristic member of the culminating forest of the eastern United States, has roots which are enveloped by saprophytic fungi; it is believed that these fungi represent the absorptive system of the tree, and it is likely also that they are able to make nitrogen available, since so many similar fungi are now known to possess this power. In any event, the beech is known to depend upon the fungus, being unable to flourish without it. Obviously, then, the beech cannot appear in a successional series until its associated saprophytic fungus finds conditions requisite for its development in the soil. It is likely, too, that other saprophytic organisms are detrimental to various green plants, thus becoming a factor in their elimination. There is opened up here a great field of investigation, and all that can be stated now with definiteness is that it is likely to be demonstrated that the accumulation of humus is of profound significance in the development of successive saprophytic organisms, and probably on this account in the succession of the higher plants.

c. Toxicity.—Still another humus factor that seems likely to be of large significance, but whose exploitation is so recent that we cannot yet appraise it, is soil toxicity. It has been known for a long time that the roots of plants give off various excretions, but it is only through the recent careful work of LIVINGSTON and his associates (**22**), and later of SCHREINER and REED (**25, 26**), that we have come to know much concerning their nature and influence. In the case of wheat it has been ascertained that the roots give off certain substances which are deleterious and perhaps actually toxic, especially to wheat. Such results should not occasion surprise, since it is well known that many bacteria excrete substances which retard or even prevent the further growth of their own kind.

One of the greatest puzzles to the student of plant dynamics has been afforded by the successional series in bogs, since in spite of the wet soil there are many plants that obviously are xerophytic. There is universal agreement that there is something in bog soils

which is detrimental to plant growth, but there have been various theories as to its nature. Some years ago LIVINGSTON (**23**) discovered that bog waters have an effect on the growth of algae which is quite comparable to the effect of various toxic agents. More recently DACHNOWSKI, following the lead suggested by SCHREINER and REED, has been making a careful study of bog toxins (**27, 28**). On account of the poor drainage of bogs, there is no other habitat where root excretions would be more likely to remain. Year by year these excreta would accumulate, thus making the bog more and more unfitted for the development of ordinary hydrophytes; hence for a time the dominating bog plants would be those which would be able to withstand the acids and other deleterious excreta given off by the roots or produced subsequently by changes in the accumulating humus. However, when these bog xerophytes bring the humus level well above the water table, the deleterious plant products will be more and more oxidized, and ultimately there will be produced a soil of such character that ordinary mesophytes may flourish in it. While there is much in this theory which still requires confirmation, it certainly accounts for most bog phenomena and is not controverted by any known facts. It is likely also that some of the accumulating soil compounds may be of importance in neutralizing deleterious inorganic or organic soil constituents. In any event, the study of soil toxins and of their varied relations to plants is one of the great fields of investigation for the future.

d. Food.—Perhaps there are some who would have supposed that the chief significance of humus accumulation lies in the increased amount of plant food that thus is made available. Once it was supposed that the well known luxuriance of plants in humus is due to the large amount of plant food which it contains. Long ago this luxuriance was shown to be in the main due to other causes, but recent experiments have demonstrated that ordinary green plants are able to absorb certain foods (as glucose), and it may be that such plants actually utilize in this way some of the substances of the humus. It is likely that the increasing food supply in accumulating humus is an important factor in the succession of the soil organisms, but as yet this subject has never been investigated.

It also offers a fascinating field for study. The depletion of mineral foodstuffs in the soil has been urged as a successional factor, but it is doubtful if this is of any consequence. The great abundance of the mineral constituents of plants in nearly all soils is in strong contrast to the minute amounts which the plants contain. Furthermore, the plants in their decay return to the soil the mineral elements which they took from it.

e. Temperature and aeration.—Finally humus accumulation alters the soil temperature and the air content of the soil. For the most part changes in air content and in temperature probably are insufficient to be of great influence in vegetative change. In bogs, however, there is evidence that each of these factors is of importance. TRANSEAU has shown (**24**) that in the growing season the temperature of the water and of the soil in bogs is below that of other soils, and of the superincumbent air. Such a condition certainly is detrimental to root activity. Similarly TRANSEAU (**24**) has shown that the lack of aeration in bog soils is detrimental to root activity. Thus for these reasons (and probably also because of soil toxicity, as noted above) certain stages in bogs are characterized by the development of a xerophytic vegetation, since the unfavorable conditions for root absorption make existence in bogs difficult for any plants with aerial organs except such as have structures which reduce transpiration. That such bog plants are actual and not merely apparent xerophytes was demonstrated in brilliant fashion by TRANSEAU (**24**), who produced plants with xerophytic structures from ordinary plants by growing them in bog conditions.

C. SHADE

Next in importance to humus among the dynamic biotic agencies is shade. The foresters have known for generations that in the reforesting of a region the first trees to appear are those which require a large amount of sunlight for their development; conspicuous among such light-requiring pioneers are the poplars and birches. Rarely is a dense growth of these trees followed by trees of similar kind, since the increasing shade makes the development of seedlings of these species more and more difficult. Other trees, however, perhaps pines and oaks, are able to thrive in a degree of

shade which aspens and birches might not be able to endure. Finally the pines and oaks in turn may be succeeded by such trees as the beech, the sugar maple, and the hemlock, since these trees are able to develop in a considerable amount of shade. The latter trees may continue indefinitely, unless climatic or topographic changes intervene, since, unlike most species of trees, their seedlings are able to develop in shade as dense as that which is cast by the parent trees. While the influence of increasing shade, as here set forth, is undoubted, the extent of its influence is not known; *pari passu* with the increase of shade, and partly on account of it, there goes on the accumulation of humus. On uplands in our climate each of these factors tends to bring about the development of a mesophytic forest, but as yet it is impossible to determine which has the more potent influence. Increasing shade favors the mesophytic trend of upland successions in yet another way than through its direct influence and through its effect upon humus accumulation; the cutting off of light results in increased atmospheric humidity and hence in decreased evaporation. Some recent observations by FULLER (**29**), as yet unpublished, show that the pioneer plant formations of the Indiana sand dunes are characterized by high evaporation, and that this evaporation progressively decreases until the minimum is reached in the climatic forest.

In contrast to ordinary uplands is the influence of light upon the development of vegetation in lakes. At the outset there are many lakes which are too deep to have a conspicuous vegetation of green plants on the bottom. Through the accumulation of inorganic détritus and of humus, the latter arising from the decay of green plants living in the upper waters and from the decay of other organisms at all levels, there gradually is made possible the development of a plant formation on the bottom, composed of plants which require only a miminum amount of light. In succeeding years the shallowing of the lake makes possible a greater and greater development of green herbage, unless the development of a rich floating vegetation again cuts off the light. It is obvious that the influence of light and shade on succession is not so explicitly related to life as is that of humus; humus can arise only from organisms, but shade may be cast by many other things than trees. The rapid develop-

ment of a mesophytic forest in a canyon is due in large part to the increasing shade which is cast by the walls as the canyon deepens. However, the predominating influence of shade certainly is in connection with forest development, and hence it is not unfair to group it with biotic influences.

D. PLANT INVASION

A further biotic influence is that of plant invasion. In the long period of geologic history, plant migrations from one region to another must have played a tremendous part in the changing aspect of vegetation. There is reason to believe, however, that such changes, apart from those due to human influence, have been wrought almost as slowly as those due to climatic change. So imperceptibly do these migrations take place that we know of no profound change that has been wrought by this means in natural floras within historic time.

E. MAN

The last of the biotic influences to be considered is that of man. Most of the factors hitherto considered, especially increasing shade and accumulating humus with its varied kinds of influence, cooperate to transform originally hydrophytic and xerophytic plant formations into those that are more mesophytic; that is, they institute progressive successions. The influence of man, however, almost without exception, is retrogressive. Human culture reaches its highest expression in mesophytic climates or on mesophytic soils; the xerophytic soils of rocky crags and of sand barrens are unfavorable places for human exploitation, and the desert is for man an unprofitable waste, except where he finds an oasis or makes a district mesophytic through irrigation. Similarly, the waters are of value chiefly as avenues of transportation and as a source of food, not as a habitation; and swampy tracts are considered valueless, unless made mesophytic by drainage. Man, therefore, in seeking a place of abode, in clearing land for agriculture, and in his search for timber, has destroyed chiefly mesophytic vegetation, in other words, the very vegetation which, in most areas occupied by human culture, has been seen to be the culminating plant formation.

When a forest is destroyed by cutting, the succeeding vegetation commonly is more xerophytic than that which was destroyed, because of increased light and decreased humus. The influence of fires is much more retrogressive, because the vegetation of the forest floor, as well as the trees, is destroyed, and also because the humus is more largely oxidized. Both in such areas as these which gradually return to the forest, and in other areas which are prevented from making such return, on account of their use for cultivation, or for habitation, or for grazing animals, there enter among the pioneers a large number of cosmopolitan weeds which follow in the train of man. Most of these weeds are of xerophytic tendencies, and hence are well fitted for these pioneer stages. In the revegetation of fallow land and in reforestation, these immigrants soon disappear, giving way before the returning native forms which inhabited the region before man entered with his destructive axe and torch.

F. PLANT PLASTICITY

Before concluding this section on biotic agencies, there should be noted some instances where dynamics in the habitat meets with a reaction other than that of succession. Very frequently in the draining of a pond by humus accumulation, the same plants may be found in different stages, but characterized by a change of aspect. For example, the mermaid weed (*Proserpinaca*), the water hemlock (*Sium*), and the water smartweed (*Polygonum amphibium*) are fitted for existence in a shallow pond and also in a swamp where the soil level is above the water table. In the former instance the plants possess so-called water leaves, which vary greatly in form and structure from the air leaves, which are seen in the following swamp stage. Such amphibious plants thus have the power through their great plasticity of existing in two distinct plant formations; many of their companions, however, in the two situations are quite unlike, indicating that the habitat range of the latter is narrower, on account of their smaller plasticity.

In the western forests, the Douglas spruce may be a xerophytic pioneer, and yet may remain through all the stages of forest development, including the culminating mesophytic forest; this remark-

able tree may even dominate in each of the stages. The Douglas spruce differs from the amphibious plants in that it exhibits no such striking changes in leaf habit in the different conditions in which it lives; however, the change in the accompanying vegetation is much more profound than in the swamp, for at the outset the Douglas spruce may be accompanied by xerophytic pines and junipers, and at the close by the mesophytic hemlock and by a luxuriant carpet of mesophytic ferns and mosses. Thus it is clear that the life range of some plants is very broad and of others very narrow; obviously the latter are the best markers of habitat dynamics, for with a change of conditions they soon give way to other forms. Of especial interest to the physiologist is the situation in such plants as the Douglas spruce, whose leaves without change of form or structure seem equally fitted for light or shade, for dryness or humidity.

7. Conclusion

It is not to be supposed that all the influences which are involved in plant succession have been outlined in the preceding pages. Indeed, some minor contributory factors have been purposely omitted, because of the brief time allotted upon such an occasion. However, it is to be hoped that the dominating factors, so far as known at present, are here mentioned. From a survey of the various agencies involved, it seems clear that the influences which bring about succession differ profoundly in their nature, and also in the rapidity of their action. Although they grade into one another as do all phenomena of nature, we may recognize climatic agencies, which institute vegetative cycles whose duration is so long that the stages in the succession are revealed only by a study of the record of the rocks. Within one climatic cycle there may be many cycles of erosion, each with its vegetative cycle. The trend of such a cycle can be seen by a study of erosive processes as they are taking place today, but the duration of the cycle is so long, that its stages can be understood only by a comparison of one district with another; by visiting the parts of a river from its source to its mouth, we can imagine what its history at a given point has been or is to be. Within a cycle of erosion there may be many vegetative cycles, and among these are some whose duration is so

short that exact study year by year at a given point makes it possible to determine not only the trend of succession, but the exact way in which it comes about. We can see one stage replacing another before our eyes, and hence we may hope some day, if we exercise sufficient ingenuity and patience, to understand the underlying causes of the change. It is clear therefore that vegetative cycles are not of equal value. Each climatic cycle has its vegetative cycle; each erosive cycle within the climatic cycle in turn has its vegetative cycle; and biotic factors institute other cycles, quite independently of climatic or topographic change. It is small wonder that within this complex of cycle within cycle, each moving independently of the others and at times in different directions, dynamic plant geography has accomplished so little in unraveling the mysteries of succession. It may be some small contribution to this end, if the preceding considerations assist in delimiting the problems.

THE UNIVERSITY OF CHICAGO

LITERATURE CITED

1. KING, WILLIAM, Of the bogs and loughs of Ireland. Phil. Trans. Roy. Soc. London **15**:948–960. 1685.
2. BUFFON, G. L. L., Mémoire sur la culture des forêts. Hist. Acad. Roy. Sci. Paris 1742:233–246.
3. BIBERG, I. J., Oeconomia naturae. Amoen. Acad. **2**:1–52. 1749.
4. DUREAU DE LA MALLE, A. J. C. A., Mémoire sur l'alternance ou sur ce problème: la succession alternative dans la reproduction des espèces végétales vivant en société, est-elle une loi générale de la nature? Ann. Sci. Nat. I. **5**:353–381. 1825.
5. STEENSTRUP, J. J. S., Geognostik-geologisk Undersögelse af Skovmoserne Vidnesdam og Lillemose i det nordlige Sjaelland, ledsaget af sammenlignende Bemaerkninger, hentede fra Danmarks Skov-, Kjaer- og Lyngmóser i Almindelighed. Dansk. Vid. Selsk. Afhandl. **9**:17–120. 1842.
6. FORBES, EDWARD, On the distribution of endemic plants, more especially those of the British Islands, considered with regard to geological changes. Brit. Assoc. Rep. **1845**^{2}:67–68.
7. VAUPELL, C., De nordsjaellandske Skovmoser. Copenhagen. 1851.
8. REISSEK, S., Ueber die Bildungsgeschichte der Donauinseln im mittleren Laufe dieses Stromes. Flora **39**:622–624. 1856.
9. VAUPELL, C., De l'invasion du hêtre dans les forêts du Danemark. Ann. Sci. Nat. Bot. IV. **7**:55–86. 1857.

10. GREMBLICH, J., Pflanzenverhältnisse der Gerölle in den nördlichen Kalkalpen. Ber. Bot. Ver. in Landshut. **5**:15–31. 1876.
11. HULT, R., Försök till analytisk behandling af växtformationerna. Meddel. Soc. Faun. Flor. Fenn. **8**:1–156. 1881.
12. TREUB, M., Notice sur la nouvelle flore de Krakatau. Ann. Jard. Bot. Buitenzorg **7**:213–223. 1888.
13. WARMING, E., De psammophile Formationer i Danmark. Vid. Med. Naturh. For. Copenhagen **1891**:153–202.
14. FLAHAULT, C., et COMBRES, P., Sur la flore de la Camargue et des alluvions du Rhône. Bull. Soc. Bot. France **41**:37–58. 1894.
15. WARMING, E., Plantesamfund; Grundträk af den ökologiske Plantegeografi. Copenhagen. 1895 (German edition, 1896).
16. GRAEBNER, P., Studien ueber die norddeutsche Heide. Bot. Jahrb. **20**:500–654. 1895.
17. MEIGEN, F., Die Besiedelung der Reblausherde in der Provinz Sachsen. Bot. Jahrb. **21**:212–257. 1896.
18. COWLES, H. C., The ecological relations of the vegetation on the sand dunes of Lake Michigan. BOT. GAZETTE **27**:95–117, 167–202, 281–308, 361–391. 1899.
19. ———, The physiographic ecology of Chicago and vicinity; a study of the origin, development, and classification of plant societies. BOT. GAZETTE **31**:73–108, 145–182. 1901.
20. ———, The influence of underlying rocks on the character of the vegetation. Bull. Amer. Bur. Geog. **2**:163–176, 376–388. 1901.
21. CLEMENTS, F. E., The development and structure of vegetation. Bot. Surv. Nebr. VII. Studies in the vegetation of the state. III. 1904.
22. LIVINGSTON, B. E., BRITTON, J. C., and REID, F. R., Studies on the properties of an unproductive soil. U.S. Dept. Agric., Bull. Bur. Soils 28. 1905.
23. LIVINGSTON, B. E., Physiological properties of bog water. BOT. GAZETTE **39**:348–355. 1905.
24. TRANSEAU, E. N., The bogs and bog flora of the Huron River Valley. BOT. GAZETTE **40**:351–375, 418–448. 1905; **41**:17–42. 1906.
25. SCHREINER, O., and REED, H. S., Some factors influencing soil fertility. U.S. Dept. Agric., Bull. Bur. Soils 40. 1907.
26. ———, The production of deleterious excretions by roots. Bull. Torr. Bot. Club **34**:279–303. 1907.
27. DACHNOWSKI, A., The toxic property of bog water and bog soil. BOT. GAZETTE **46**:130–143. 1908.
28. ———, Bog toxins and their effect upon soils. BOT. GAZETTE **47**:389–405. 1909.
29. FULLER, G. D., Evaporation and plant succession. BOT. GAZETTE **51**: (unpublished). 1911.

STUDIES ON JAMAICAN HYMENOPHYLLACEAE

FORREST SHREVE

(WITH EIGHT FIGURES)

The Hymenophyllaceae, or filmy ferns, are one of the most hygrophilous groups of terrestrial plants, and possess a number of features of anatomy and physiology in common with aquatics and the bryophytes. Although mainly restricted to tropical and subtropical regions with heavy rainfall and to habitats of high humidity, yet some of the species grow as epiphytes in company with bromeliads and succulent orchids, a fact which attracted the writer to a study of their local distribution and the gross physiology of their relation to water supply and atmospheric humidity.

The results presented in this paper were secured at the Tropical Station of the New York Botanical Garden at Cinchona, Jamaica, chiefly during the spring of 1906, while the writer was holding the Adam T. Bruce Fellowship in the Johns Hopkins University, and partly in the summer of 1909 during several months' absence from the Desert Laboratory. Cinchona is at an altitude of 1525 m. and is hard by the virgin rain forest, in which the Hymenophyllaceae attain to a wealth in species and individuals which cannot be far surpassed in any other place in the world. Of the 459 species credited to the family by CHRISTENSEN in the *Index Filicum*, 49 occur in Jamaica, and 34 of these have been available for study and observation.

Distribution

VERTICAL AND REGIONAL DISTRIBUTION IN JAMAICA.—JENMAN[1] lists for Jamaica 23 species of *Hymenophyllum* and 26 of *Trichomanes*. For 31 of the total number of species he states the vertical distribution as based on his long experience in collecting in various parts of the island. His statements indicate that there are but 5 species found only below 915 m. altitude, and 17 found only

[1] JENMAN, G. S., Synoptical list of Jamaican ferns. Bull. Bot. Dept. of Jamaica, nos. 18 and 20. 1890.

above 1220 m. The number of species (of the 31) to be expected at the different altitudes is as follows:

305 m.	610	915	1220	1525	1830	2135
10	19	19	21	31	27	20

It is in the unbroken forests of the windward slope of the Blue Mountains, at about 1525 m. altitude, that the Hymenophyllaceae are richest in species, and it is there too that they are most numerous in individuals, forming a far more conspicuous element of the vegetation than at higher or lower elevations. The most abundant and characteristic species at 1525 m. are:

Hymenophyllum fucoides Sw.[2]
Hymenophyllum asplenioides Sw.
Hymenophyllum ciliatum Sw.
Hymenophyllum polyanthos Sw.
Hymenophyllum lanatum Fee
Hymenophyllum axillare Sw.
Hymenophyllum lineare Sw.
Hymenophyllum sericeum Sw.
Hymenophyllum catherinae Hook.
Trichomanes crispum L.
Trichomanes rigidum Sw.
Trichomanes crinitum Sw.
Trichomanes radicans Sw.
Trichomanes pyxidiferum L.
Trichomanes capillaceum L. (*T. trichoideum* Sw.)

In virgin forest along the banks of the Mabess River, at about 1100 m. altitude on the windward side of the island, the writer has seen rich growths of Hymenophyllaceae, which were made up, however, solely of *Trichomanes Hookeri* Presl. (*T. muscoides* Sw.) and *T. pyxidiferum* L. Near the summit of Mount Diablo, at 600 to 700 m. altitude in the central limestone district of Jamaica, the Hymenophyllaceae are relatively rare, and must be sought carefully to be found at all. The only species observed there by the writer were:

Hymenophyllum hirtellum Sw.
Trichomanes Hookeri Presl.
Trichomanes sphenoides Kze.
Trichomanes crispum L.
Trichomanes arbuscula Desv. (*T. Bancroftii* Hook. & Grev.)

[2] The nomenclature used is that of CHRISTENSEN'S *Index Filicum*. The writer's collection of Hymenophyllaceae was determined by the late Dr. L. M. UNDERWOOD of Columbia University.

The writer has been told by Mr. WILLIAM HARRIS that in collecting at Dolphin Head, in the extreme west end of Jamaica at 550 m. altitude, he observed only two species:

Trichomanes sphenoides Kze. Trichomanes arbuscula Desv.

On passing upward in the Blue Mountains from 1525 m., the Hymenophyllaceae are found to become fewer in both species and individuals. There is but a single form found only above 1830 m. (*Hymenophyllum antillense* Jenm.), while other species common and characteristic above this altitude are:

Hymenophyllum tunbrigense Sm.
Hymenophyllum fucoides Sw.
Hymenophyllum asplenioides Sw.
Hymenophyllum polyanthos Sw.
Hymenophyllum lineare Sw.
Hymenophyllum lanatum Fee
Hymenophyllum hirsutum (L.) Sw.
Hymenophyllum sericeum Sw.
Trichomanes crispum L.
Trichomanes pyxidiferum L.

Judging by the ten-year rainfall record[3] for Blue Mountain Peak (2264 m.) and by hygrograph records obtained by the writer at Sir John Peak (1890 m.), the conditions of rainfall and humidity are no less favorable for the filmy ferns at the higher altitudes than at 1525 m.; indeed the percentage of cloudiness would appear from casual observations to be greater on the highest ridges and peaks. The mean annual temperature at Cinchona is 16° C., while that at Blue Mountain Peak may be closely approximated from a record of the monthly absolute maximum and minimum at that point to be 12° C. Although there are but few alpine features impressed upon the vegetation as a whole at the highest altitudes, yet the less abundance of the Hymenophyllaceae must be referred to the slightly lower range of temperatures rather than to less favorable conditions of rainfall and humidity. The scarcity of species and individuals at low altitudes and at such localities as Mount Diablo and Dolphin Head, in the drier portions of the island, is obviously due to the lower rainfall, humidity, and cloudiness as contrasted with the Blue Mountain forests. Where Hymenophyllaceae occur at all below 915 m., or upon the drier leeward slopes of the Blue Mountains at greater elevations than this, they

[3] All climatological data for long periods are taken from the records of the Department of Public Gardens and Plantations of Jamaica.

are confined to spots where the conditions are made favorable by very local topographic or related causes; on rocks near to waterfalls, about the bases of trees in deep shade, and on the lower sides of moss-covered logs the conditions of humidity and water-supply resemble locally the climatic conditions of the mountain forests. The Hymenophyllaceae which occur at low altitudes are chiefly small species of *Trichomanes* which have a creeping rhizome and simple or pinnatifid leaves not exceeding 3 cm. in length. The forms which do not range above 914 m. are all of the description:

Trichomanes punctatum Poir.
Trichomanes sphenoides Kze.
Trichomanes polypodioides L.
Trichomanes Krausii Hook. & Grev.
Trichomanes membranaceum L.

CLIMATIC CONDITIONS IN THE RAIN FOREST.—Some notion of the climatic conditions in the zone of maximum occurrence of the Hymenophyllaceae may be had from the series of records kept at Cinchona since 1871. The position of Cinchona on the leeward slope of the main ridge of the Blue Mountains, together with the exposure of the instruments in an open lawn, keeps this record from giving a full indication of the moistness of the rain forest itself. The writer judges from personal experience that the rainfall is between 20 and 30 per cent greater and the number of rainy days between 10 and 15 per cent greater in the forests than is indicated in the following figures for Cinchona:

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Year
Rainfall . . .	7.26	4.09	5.32	6.36	11.10	8.00	3.89	8.29	9.22	18.57	12.32	11.11	104.77
Ry. days . .	14.1	12.5	12.8	12.9	18.1	13.5	10.8	11.2	16.1	21.4	18.3	16.2	179.4
Humid. . . .	84.1	83.1	83.9	83.4	85.2	84.8	79.6	80.4	84.4	88.9	86.0	86.3	84.1

In the course of some general work on the Blue Mountain region not yet published, the writer had occasion to expose a combined thermograph and hygrograph in a number of localities, and the record sheets figured herewith give a graphic conception of the daily march of temperature and humidity under natural forest conditions. The instrument was supported on an open framework one meter above the ground and sheltered by a canvas cover spread widely above it so as to keep off rain but permit a good circulation

of air. The sheet shown in fig. 1 was obtained in the forest at New Haven Gap during the week of April 16–22, 1906, and that

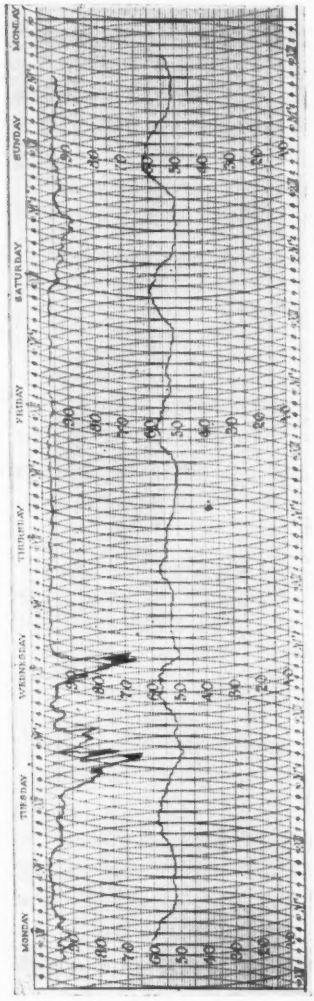

FIG. 1.—Record of temperature (the lower trace) and humidity on the floor of the rain forest at 1725 m. altitude.

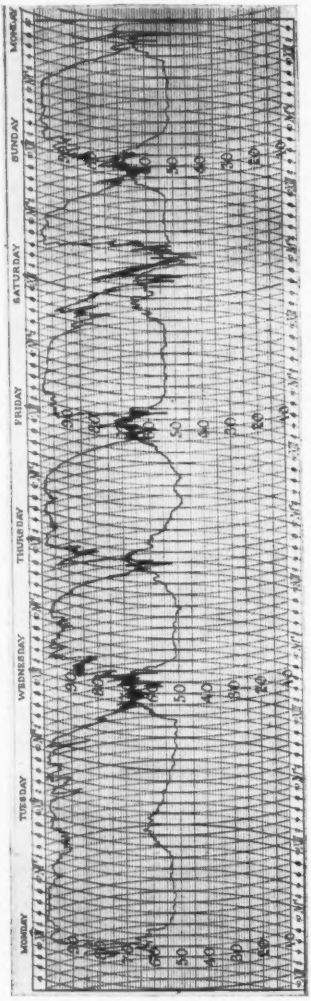

FIG. 2.—Record of temperature and humidity in a clearing in the rain forest at 1725 m. altitude.

in fig. 2 in a clearing in the forest about 200 m. distant during the preceding week. The weather of the two weeks happened to be

closely similar, and the difference in the curves of humidity brings out strikingly the degree to which the conditions on the forest floor differ from the general climatic conditions of the region. Epiphytic vegetation in the canopy of the forest is subjected to fluctuations in humidity similar to those of the clearing, together with the slightly higher range of temperatures. The high and constant humidity conditions indicated in fig. 1 are characteristic of the deep forests of ravines and lower slopes throughout the Blue Mountain region from 1200 m. to the highest peaks, while the more open forests of the upper slopes and ridges have a climate approaching more nearly that of the opening.

LOCAL DISTRIBUTION OF THE HYMENOPHYLLACEAE.—SCHIMPER[4] has pointed out the distinctness in the character of the epiphytic vegetation near the forest floor and in the tops of the highest trees as observed by him in the forests of Trinidad and Venezuela. There the lowest epiphytes in the forest are tender hygrophilous plants which show no structural adaptations to the epiphytic habit and are often found as terrestrial plants. On the higher limbs and twigs of the largest trees are found xerophilous and succulent epiphytes possessing marked specialization in structure and in the ecology of reproduction. The Jamaican rain forest region has a highly developed erosion topography. Only in the ravines does the vegetation approach the stature and luxuriance of such lowland forests as were visited by SCHIMPER, and in them may be observed the same contrast in the character of the epiphytic vegetation. On the slopes, ridges, and peaks the forest trees are not so tall by one-half as in the ravines, and the canopy is much more open, particularly on the ridges and peaks. This results in the forests of the upper slopes being devoid of the epiphytes of the lowest levels of the ravine forest, while on the ridges and peaks the epiphytes which are characteristic of the canopy of the ravine forest may be found growing down to the forest floor. In other words, the trees of the upper slopes have the same epiphytic flora that would be found in the upper two-thirds of the trees of the ravines, while the trees of ridges and peaks have only those that are char-

[4] SCHIMPER, A. F. W., Die epiphytische Vegetation Amerikas. Bot. Mit. aus den Trop. Heft. 1. 1888.

acteristic of the uppermost third, and the mid-height species are restricted in these habitats to the sides of prostrate trunks or fallen logs. These facts concerning the epiphytic vegetation in general are the key to the local distribution of the Hymenophyllaceae; the most important factors governing their distribution are those that have to do with the vertical differences in climate in the rain forest.

The commonest filmy ferns that are invariably rooted in the soil on the floor of the forest are *Trichomanes rigidum*, *T. radicans*, and *T. scandens*. The first of these has a short erect rootstock and its cluster of stiff leaves grows to a height of 20 cm. It is found on the floor of deep ravines or elsewhere in dense shade, and its constant wetness is well attested by the growths of epiphyllous hepatics which cover all but the youngest leaves. *Trichomanes radicans* is a climber, sometimes reaching as much as 2 m. from the ground, but only in the most moist situations. Like the foregoing species it has finely dissected leaves, the branches of which are winged with upturned leaf tissue, providing it with a ramifying system of gutters, which happen to serve well in distributing over the leaf the chance drops of water which fall from overhanging foliage.

There are a number of facultative epiphytes with erect leaves which either grow in clusters out of an erect rootstock or are spaced along a horizontal rhizome. These do not often grow in the soil itself, but are commonly found on the ground rooted in tufts of moss, on fallen logs, or on the bases of the trunks of trees. These forms are slightly tolerant of the drying off of their leaves, but they are never found over about 2 m. from the ground except in the deepest ravines. The habit of the leaves being erect, their wetting must take place from rainfall or the dripping of wet foliage; their roots, however, are very favorably situated as respects water supply. The common members of this category are: *Hymenophyllum abruptum*, *H. ciliatum*, *H. microcarpum*, *Trichomanes Hookeri*, *T. pyxidiferum*, and *T. capillaceum*. *Trichomanes capillaceum* has the most delicately cut leaves of any of the Jamaican species; and its commonest habitat is the bases of the trunks of tree ferns, where it is rooted among the coarse rhizoids of the tree fern and is

usually shaded and sprinkled by the overhanging leaves of the climbing fern *Lomaria attenuata*. *Hymenophyllum asplenioides* is quite as closely restricted to the most moist habitats as are any of the above-mentioned species, but the fact that its leaves are pendant confines its occurrence to tree trunks and rocks.

Another group of species may be characterized, which are not sharply separable from the last, but are on the whole much more

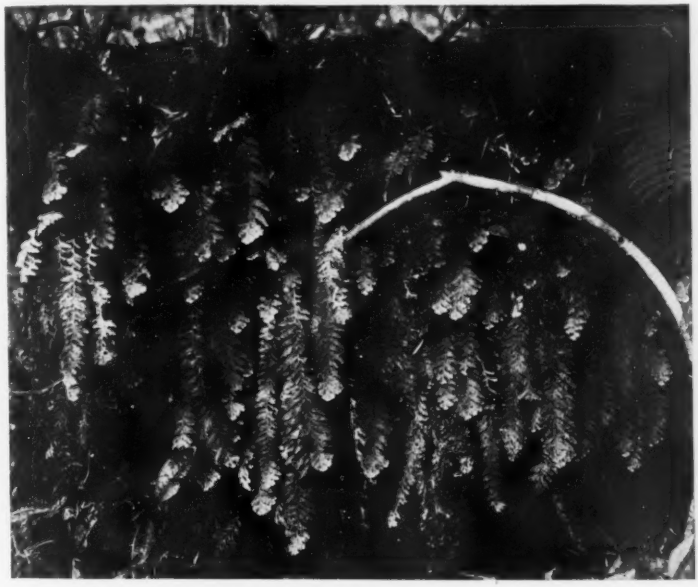

FIG. 3.—A typical colony of *Hymenophyllum sericeum*, pendant from a horizontal limb bearing mats of *Ptilidium*; one-fourth natural size.

capable of enduring desiccation and insolation. They are never found on the floor of the forest in ravines nor as low-growing epiphytes there, but are mid-height epiphytes in ravines and are found on the lowest layers of the slope forests. Their leaves are erect and glabrous, growing singly along a creeping rootstock and not exceeding 10 cm. in length in any species. These are *Hymenophyllum polyanthos*, *H. fucoides*, *H. catherinae*, *H. tunbrigense*, and *Trichomanes crispum*. *Hymenophyllum polyanthos*

FIG. 4.—A tree in the drier rain forest of the leeward slopes of the Blue Mountains, with epiphytic colonies of *Hymenophyllum sericeum* growing up to 6 m. from the ground.

is the commonest filmy fern in Jamaica, and, with the exception of the hairy forms to be mentioned, it is the most capable of resisting desiccation of any of the species. On losing water its pinnae curl downward and the midrib itself then curls, so that the whole leaf tends to close into a form resembling the circinate shape of a young leaf. *Hymenophyllum fucoides* and *H. catherinae* have also characteristic modes of curling up on becoming relatively dry. The writer has seen the rain forest on exceptionally bright days, when the humidity had fallen to 60 per cent, when every plant of these three species was curled in a marked degree. The curling is not at all in such a manner as serves to protect any part of the leaf from further desiccation.

The three pendant hairy forms *Hymenophyllum sericeum*, *H. lanatum*, and *H. hirsutum* are the most resistant to drying and insolation of any of the filmy ferns. Their pendant habit confines them to the sides or bottoms of logs and leaning trunks, and they are most flourishing just beneath large clumps of mosses and hepatics, which serve as reservoirs from which supplies of water may be secured for several days after a rain. *Hymenophyllum sericeum* is not common in the topmost limbs of trees, probably through the lack of the moss substratum, but it grows in situations where it must often be subjected to two or three hours of sunshine on clear days, and it sometimes occurs as much as 12 m. above the ground in slope forest (figs. 3, 4). As the leaves grow the old pinnae die off, so that it is not an uncommon thing to find a naked rachis 30–40 cm. long with a dozen pairs of young pinnae at the tip. There are two hairy pendant species of *Trichomanes*, *T. lucens* and *T. crinitum*, but they are not at all resistant to desiccation. They are almost confined to the under sides of rotting logs, where they are rooted in the log itself and sheltered from rain and the drip from foliage. The writer has seldom seen wet leaves in nature in either of these species, both of which have a metallic gray-green color. Their physiology has not been investigated.

Physiology

ROOT-ABSORPTION.—In order to test the ability of the various species of Hymenophyllaceae to secure by root-absorption all the

water required in a humid atmosphere, a number of individual plants or clumps of plants with undisturbed substratum were brought into the laboratory and the leaves allowed to dry off, but not to curl through too great loss of water. The plants were then placed under bell jars in which the humidity was kept above 90 per cent, and the roots wetted every day or two without wetting the leaves. It was not necessary to take any precautions against condensation of moisture on the leaves, for whenever the atmosphere in the bell jars approached saturation there was immediate condensation on the cool walls of the jar, lowering the humidity. The following data record the result of this test:

Trichomanes rigidum lost turgor in 5 days; dead in 14 days.
Trichomanes radicans remained normal for 40 days, with the chloroplasts on the lateral walls.
Hymenophyllum microcarpum remained nearly normal for 40 days, some groups of cells having become disorganized.
Hymenophyllum ciliatum remained normal for 40 days.
Trichomanes capillaceum remained normal for 40 days.
Hymenophyllum asplenioides remained normal for 40 days.
Hymenophyllum polyanthos remained normal and grew for 40 days.
Hymenophyllum sericeum remained normal and grew for 40 days.

The only form in this series incapable of maintaining its turgidity (*Trichomanes rigidum*) has already been stated to be one of the most hygrophilous, and those capable of growing under the conditions of the experiment the least hygrophilous of the Jamaican species. The extremely low water loss from surface-dry leaves in a very moist atmosphere can be met, therefore, by root-absorption and conduction in all but the most pronouncedly moisture-loving species. There are certainly no other common species which rank with *Trichomanes rigidum* in this respect; even the extremely delicate *T. capillaceum*, also requiring the most moist habitats, when kept subsequently under the conditions of this test maintained a normal condition for 35 days, at the end of which time the experiment had to be discontinued.

The conduction of root-absorbed water to the leaves is through a vascular system very poorly developed as respects the number and size of the water vessels, and the path of the water from the veins of the leaf to the transpiring cells lies through other cells, perhaps

only as many as 4 or 5 in the finely dissected forms, but as many as 10 in *Trichomanes crispum* or 25 in the simple leaves of *Trichomanes Hookeri*. In *Trichomanes rigidum* the number of walls between the vessels and the marginal cells is 6–8, but an examination of the lateral walls shows them to have a peculiar thickening, which gives the central part of each one as seen in section the appearance of having a double convex lens inserted in it (fig. 5). These ridges occur in the lateral walls throughout the leaf, so as to provide the leaf with a rigid meshwork which is calculated to strengthen it in very much the same way that a piece of wire glass is strengthened by the wire netting imbedded in it. Although at every point in the lateral walls there are areas of thin wall above and below the

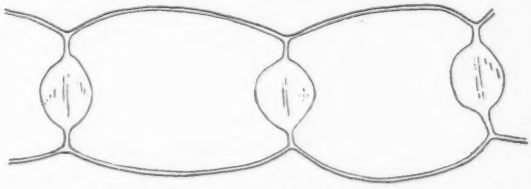

FIG. 5.—Vertical section of the leaf of *Trichomanes rigidum*, to show the mechanical thickening of the lateral walls; ×764.

thickening, yet it can be readily seen that the thickenings serve to hinder the transfer of water from cell to cell, and may be accountable for the inability of this species to secure root-absorbed water quickly enough to meet even the demands of transpiration in a nearly saturated atmosphere. Although *Trichomanes capillaceum* is quite as hygrophilous a form as *T. rigidum*, it has to its advantage as respects water movement in the leaf the fact that its marginal cells are never more than 4 or 5 cells removed from the veins, and also that in its slightly thickened walls there are intercellular passages, capable of functioning as avenues for the ready transfer of water.

TRANSPIRATION.—For the measurement of transpiration in the Hymenophyllaceae the only method available is that of the potometer, which admits of having the leaf surface wet or dry. Attempts to use entire plants on the potometer were not satisfactory, and the slenderness of the petioles of most forms, together

with the smallness of the leaves in others, excluded from use all but *Trichomanes crispum*, *T. radicans*, and *T. rigidum*. Similar mechanical difficulties made it impossible to investigate the root pressure, so it is not possible to state what relation the facts ascertained by the potometer method as to the intake of water by transpiring leaves may bear to those which hold true for intact plants in a state of nature. In plants in which the transpiring surface is also capable of absorption, and in which there is no structural nor functional means by which transpiration is limited or regulated, it is to be expected that the rate will be largely a function of the conditions governing evaporation.

A single leaf of *Trichomanes crispum*, freshly cut from the plant and mounted on the potometer, was placed under a bell jar and kept wet by a drip from an opening in the top of the jar. There was no forward movement of the bubble in the potometer tube during the nine hours through which the test was run. In one of the two repetitions that were made there was a backward movement of the bubble at the rate of 1 mg. per hour during the early afternoon, suggesting a backward movement of water in the vessels due to the absorbing activity of the leaf surface. In order to compare the behavior of leaves only partially wet, the test was repeated so as to have the leaf wet at the start but without drip to keep it so. The following figures are the total losses in mg. for the intervals indicated:

11:00 A.M., leaf partly wet	
12:15 P.M., leaf just dry	73.5
1:15 P.M., leaf beginning to curl	61.0
1:16 P.M., leaf wetted again	
2:45 P.M., leaf beginning to dry off	4.0

Similar results were obtained with *Trichomanes radicans*. Neither in the dull diffuse light used in all other experimentation with the Hymenophyllaceae nor in bright diffuse light did thoroughly wet leaves show an intake of water through the petiole. A single test was made with a partially dry leaf of this species. The leaf had been mounted on the potometer since 9:00 A.M. and kept wet until evening. At 5:30 P.M. the drip was stopped and the bell jar left over the leaf during the night. At 9:00 the next morning

the leaf was partly dry, but not sufficiently so for the tips of the pinnae to have begun to curl, and the basal pinnae were still wet. The intake of water during the $15\frac{1}{2}$ hours was 39 mg.

The backward movement of the bubble in the test with *Trichomanes crispum* suggested determining the behavior of a leaf kept completely wet for several days. *Trichomanes rigidum* was used in this experiment, and in order to prevent any portion of the leaf from becoming dried the whole was submerged under a water-tight bell jar in the manner shown in fig. 6. The following figures show a continuous and uniform retreat of the potometer bubble:

		Readings	Amts. per hr.
Oct. 31,	10:50 A.M.	65.5	
Oct. 31,	2:15 P.M.	63.5	0.60
Nov. 1,	9:00 A.M.	59.5	0.24
Nov. 1,	3:00 P.M.	57.8	0.26
Nov. 1,	6:00 P.M.	57.0	0.26
Nov. 2,	9:00 A.M.	54.0	0.20
Nov. 2,	12:00 noon	53.0	0.33
Nov. 3,	10:00 A.M.	47.3	0.26
Nov. 3,	12:00 noon	46.5	0.40
Nov. 3,	3:15 P.M.	45.5	0.30
Nov. 3,	6:15 P.M.	44.5	0.33
Nov. 4,	9:00 A.M.	40.5	0.27
Nov. 4,	12:00 noon	39.5	0.33
Nov. 4,	3:00 P.M.	38.5	0.33

That the pressure of the water surrounding the leaf had to do with this retreat is scarcely probable, in view of the hourly rate at night being always less than by day. While an intake of the amount here observed would be impossible in intact plants without exudation at the roots, the experiment gives an excellent demonstration of the absorbing power of the leaves, and the greater amounts absorbed by day than by night point to an influence exerted by photosynthetic activity on the absorption rate.

The extreme slenderness of the petioles of the ferns most capable of resisting surface dryness made it impossible to experiment with them on the potometer, but the experiments on root-absorption indicate that those forms are capable of maintaining a regular transpiration rate when atmospheric conditions do not make it too rapid.

The work of POND[5] and the more recent work of THODAY and SYKES[6] goes to show that submerged aquatics absorb, and presumably exude, considerable quantities of water. Each of the two methods employed by POND showed absorption by the normal root system; the method of THODAY and SYKES showed an intake by cut shoots. The writer has not made any experiments with the

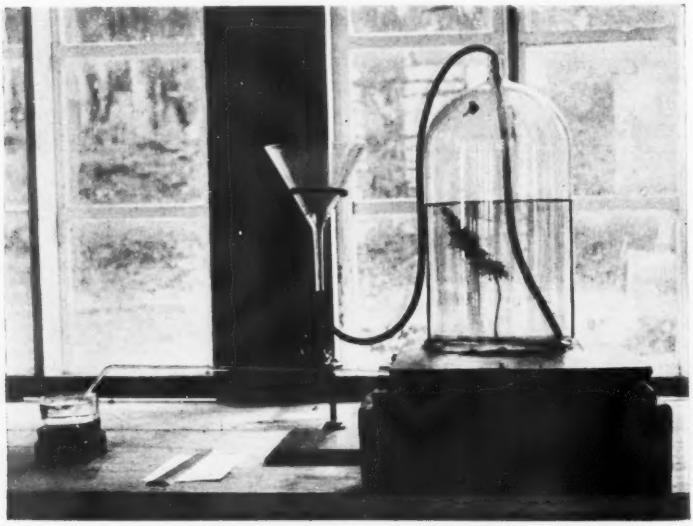

FIG. 6.—Form of apparatus used in determining the rate of leaf-absorption of water.

Hymenophyllaceae to ascertain if intact plants absorb with their uninjured root system when the leaves are wet or submerged. No evidence can be given, in other words, which is as satisfactory as that of POND for *Ranunculus aquatilis*. THODAY and SYKES showed a rapid intake of eosin solution by the cut ends of shoots of *Potamogeton*, and, if the eosin method may be trusted, their experiments go to show that the transpiration stream is quite strong even when shoots are severed from the root system. As respects

[5] POND, RAYMOND H., The biological relation of aquatic plants to the substratum. Report U.S. Fish Comm., pp. 483–526. 1903.

[6] THODAY, D., and SYKES M. G., Preliminary observations on the transpiration current in submerged water plants. Annals of Botany **23**:635–637. 1909.

method, the writer's experiment with a single leaf of *Trichomanes* is comparable with those of THODAY and SYKES with severed shoots of *Potamogeton*. In spite of the violence which is done to the normal functioning of the leaves of flowering plants by removal from the plant (which will be shown below not to hold true of the filmy ferns), the writer is inclined, on the concordant evidence of the potometer experiments described, to believe that there is a standstill in the transpiration stream of a filmy fern when the leaves are wet. In exact analysis it is unthinkable that there should not be a simultaneous loss and intake of water through the leaf surface, but the backward movement of the potometer bubble shows that the absorbing activity is greater than the exudation when leaf-absorption is given play through the removal of the roots. In the intact plant, however, leaf-absorption is devoted solely to the maintenance of leaf turgidity, and the movement of root-absorbed water toward the leaves is in abeyance. When in its natural habitat, the filmy fern is now under aquatic conditions, now under those of a land plant. There may or may not be a transpiration stream in a plant according to the state of wetness of its leaves, and when the leaves are dry the ensuing root-absorption will or will not be able to meet the demands of water loss in the leaves according to the species and the humidity conditions in which it is placed. From the evidence given it appears that in nature there is now a slight transpiration stream in a given plant and now an intake of water by the leaves, accompanied by a cessation of conduction in the vessels.

TOTAL SUBMERGENCE.—A completely wet filmy fern is in a state equivalent to that of a submerged aquatic, excepting that it is under much more favorable conditions as respects the aeration of the water surrounding it. In order to determine what would be the effect of the stoppage of the transpiration stream for a considerable period, a number of plants were grown in total submergence, and in order to make these conditions as natural as possible the water was changed every four days and was aerated twice daily by injecting a fine stream of water with a large pipette. Flourishing individuals of the following species were selected, with their roots intact: *Trichomanes rigidum*, *T. radicans*, *T.*

crispum, *T. capillaceum*, *Hymenophyllum hirsutum*, *H. polyanthos*, and *H. sericeum*. At the close of 30 days of submergence these were all thriving, and the contents of the cells were of normal appearance under the microscope, save in the case of *H. sericeum*. Its leaves were blackened and the chloroplasts disorganized and lumped together. This most drought-resisting of the forms worked with (the one which is least often completely wet in nature) is therefore the only species incapable of assuming an aquatic rôle and having its transpiration stream stopped. Simultaneously with the above experiment, in which cistern water was used, an attempt was made to grow the same species in SACHS's nutrient solution, diluted to half-strength, with fatal results to all of the cultures within the first week.

ABSORPTION OF ATMOSPHERIC MOISTURE.—In the experiment regarding root-absorption, in which plants were kept with dry leaves in a moist atmosphere, it appeared possible that the survival of the individuals used might be in part due to the absorption of atmospheric moisture by the leaves. A test was made in which 10–15 leaves were cut from each of several species, sealed at the cut ends with vaseline, and dried at 70–80 per cent humidity until all the surface water was gone and the segments had just begun to curl. These were then laid on non-absorbent paper and placed in a small chamber kept moist with wet sheets of filter paper and clumps of sphagnum. The humidity was kept continually above 95 per cent, and was usually nearer saturation. Several pieces of iron that happened to be available were placed inside, and together with the glass top to the chamber served to catch the condensation whenever the humidity approached saturation. Although an effort was thus made to prevent actual condensation of moisture on the leaves, a slight amount of it may have taken place, but if it did it is no more than might have occurred in nature, and it failed to prevent loss of weight by some of the species used. The following series of weighings was made by removing the leaves from the non-absorbent paper and placing them between large watch glasses; as the humidity of the laboratory was seldom below 75 per cent, no great error was caused by the transfer. The first weight is that of the surface-dried leaves, the following ones being

the weights on successive days while in the chamber. The chamber was accidentally opened one night, with a resulting fall in humidity that caused a loss of weight in all the leaves in it at the time, as indicated in the table by asterisks.

	Surface-dried weight	1st day	2d day	3d day	4th day	5th day	6th day	7th day
Trichomanes rigidum	1.510	1.308	1.293	1.317	1.290	1.260	1.165	1.115
Trichomanes radicans	3.880	3.500	3.210	3.015*	2.787	2.550	2.600	.....
Hymenophyllum asplenioides	0.460	0.430*	0.450	0.480	0.522	0.530	0.650	.....
Hymenophyllum polyanthos	0.317	0.350	0.402	0.458	0.350*	0.462	.....	.....
Hymenophyllum sericeum	0.668	0.755	0.840	0.861	0.914	0.930	.....	.....

Trichomanes rigidum and *T. radicans* showed themselves incapable of even so much as maintaining their original weight and became more curled each day, while the other species showed steady gains in weight and maintained a perfectly normal appearance. The fact that these species behaved differently under the same conditions, and that the gain or loss was consistently maintained in each case, together with the fact of their behavior being in accord with their habitat preferences, gives assurance of the result being indicative of their normal behavior. The more hygrophilous species, accustomed to being covered with a film of water, fail to maintain their turgidity even in the presence of a nearly saturated atmosphere, while the high epiphytes, to one of which at least constant wetness is fatal, gain appreciable quantities of water.

In order to determine whether the hygroscopic activity of the leaves of the epiphytic species was merely a physical phenomenon, several leaves of *Hymenophyllum sericeum* were killed in chrom-acetic fixing fluid for 24 hours, washed for 24 hours, surface-dried, and proceeded with just as the living leaves had been. The following figures were obtained simultaneously with gains in living leaves in the moist box:

	Surf. dry wt.	1 day	2 days	3 days	4 days	5 days	6 days
Hymenophyllum sericeum	0.621	0.560	0.510	0.505	0.490	0.428	0.410

In case the chrom-acetic fluid might have altered the hygroscopic character of the cell walls, the same test was repeated with corrosive sublimate as the killing agent, and the same kind of result obtained. The leaves of *Hymenophyllum polyanthos* were also killed and carried through the moist chamber, with closely similar results.

An attempt was made to determine whether the hairy covering on the leaves of *Hymenophyllum sericeum* and related species performs any function in connection with water supply or conservation. The hairs cover both sides of the leaf densely, are multicellular, and made up of a basal stalk upon which are jointed (4–7) hairs about 0.5–1 mm. in length, diverging from each other and parallel to the surface of the leaf. Both the basal stalk and the radiating hairs are hollow and devoid of living contents. In surface-dried leaves and those commonly gathered in the field, the hairs are filled with air. Leaves which were submerged, with all of the occluded air squeezed out from among the hairs, were found after 24 hours to have their hairs filled with water. On observing the access of water to empty hairs beneath the microscope, it was seen to enter them at once and rapidly, until only a small bubble of air remained, which persisted for several hours. When leaves in which the hairs had been completely filled with water by long submergence were surface-dried with filter paper and hung in the open air at a humidity of 80 per cent, they were found at the end of 1 hour and 20 minutes to have lost approximately half the water contained in the hairs. Of the amount lost it is more than probable that as much escaped by evaporation from the hairs as became available to the leaf cells. In other leaves which had empty hairs and which were placed in a very moist atmosphere the gains in weight were not accompanied by a visible accumulation of water in the hairs. It appears, therefore, that the leaf hairs do not serve as reservoirs of water either in sufficient quantity or for a sufficient length of time to be of importance in that rôle. The coating of hairs as a whole is capable of retaining externally an amount of water equal to twice the weight of the surface-dried leaf, and under the conditions of evaporation of the rain forest this external water might be retained for 5–10 hours. The writer has placed

leaves under water without squeezing out the bubbles of air among the hairs, and found them still very imperfectly wetted up after 24 hours, and has watched dry leaves becoming wet during the commencement of rain in the forest, noticing that a heavy downpour of an hour's duration does not completely wet the leaves. It is a very uncommon thing even in the wettest weather to see leaves in the field which look saturated. The writer has no experimental evidence as to the possible rôle of the hairs in preventing water loss by the leaf cells themselves, but it is obvious that they do so to some extent, and also that they play a part in the ability of this species to withstand a greater amount of insolation than others do.

AUTONOMY OF THE LEAF AND ITS CELLS.—The extremely low degree of differentiation in the leaf tissue of the filmy ferns, and the fact that the same cells are at once capable of the functions of absorption, photosynthesis, and transpiration, seemed to indicate that the behavior of individual leaves when severed from the plant might be taken as a perfectly good criterion of their performance when *in situ*. As isolated leaves had been used in experimentation, it seemed desirable to determine their capacity for survival under the most favorable conditions. In order to do this leaves were taken from fresh plants of several species and hung in a moist chamber with wicks of cotton cord running from a pan of water so as to keep them constantly wet. The forms used were *Trichomanes rigidum*, *T. radicans*, *T. crispum*, *T. capillaceum*, *Hymenophyllum asplenioides*, *H. polyanthos*, and *H. sericeum*. At the end of 14 days all of these were in good condition, looking normal under the microscope, excepting *H. sericeum*, the inability of which to withstand submergence has already been noted. Its leaves had blackened and its chloroplasts become disorganized.

There being no reason to suppose that even portions of leaves would not survive equally well when removed from the whole leaf, a smaller series of leaf fragments was arranged, which were put in watch glasses of cistern water that was changed every other day. The only forms used were *Trichomanes capillaceum*, *T. rigidum*, and *T. crispum*, from each of which was taken a single pinna, a portion of a pinna 1 cm. long, and a portion 3 mm. long. The fragments were frequently examined under the microscope and were

allowed to run for 50 days. Up to the end of that time the pinnae and the 1 cm. pieces were normal in appearance in all three species, excepting that in *T. capillaceum* the cells had become disorganized for two or three rows back from the cut ends. The pieces 3 mm. long failed to maintain normal condition.

These tests indicate that separate leaves are capable of surviving and maintaining normal appearance, and that portions of leaves are also capable of doing so provided they are not so small that the disorganization which takes place at the cut edges leaves only two or three rows of cells along the center that might be expected to survive. So far as concerns the vegetative functioning of the plant, the leaves are quite independent of each other, and, when the leaf is completely wet, the individual cells are as independent as are those of a colonial alga.

The water by which the leaves of the Hymenophyllaceae are bathed in nature is usually rain water that has either fallen directly upon them or has dripped from foliage that has already been washed clean by frequent rainfall, and is therefore not capable of carrying any mineral salts to the plant. The water which is available to the roots, however, has usually been for some time in contact with epiphytic colonies of moss and flowering plants, and with the rotting leaves and bark always to be found beneath clumps of epiphytes, and I assume that it is rather rich in salts, including nitrates. The water which drips down over the leaves of pendant species is the same as that available to the roots of other species.

Plasmolysis with NaCl gave the following values for the osmotic strength of the sap of a few of the common species: *Trichomanes rigidum*, *T. radicans*, *T. crispum*, and *Hymenophyllum sericeum*, 0.428 N; *Hymenophyllum asplenioides* and *H. elegantissimum*, 0.514 N.

THE CHLOROPLASTS.—The chloroplasts of the filmy ferns are spherical and somewhat smaller than in most other groups of ferns. In all the Jamaican species they lie normally in a single densely packed layer next the two outside walls of the leaf cells (fig. 7). There is rarely a difference in their abundance on the two sides of the leaf.

A paleness in the coloration of the leaves of *Trichomanes radi-*

cans frequently observed in the field was found to be due to a retreat of a large proportion of the chloroplasts to the lateral walls of the cells, a performance that was afterward noticed in experiments with this and other species when isolated leaves were surface-dried and kept without access of water in a moist chamber, and also in rooted plants of *Trichomanes rigidum* which were dry as to the leaves. On the presumption that illumination was the principal factor involved in the movement of the chloroplasts, plants of several species were placed in bright diffuse light and in direct sunlight,

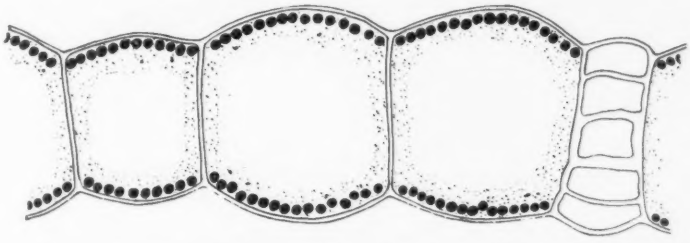

FIG. 7.—Vertical section of the leaf of *Trichomanes Hookeri*, to show the distribution of the chloroplasts and the size of the sap vacuole in a non-specialized form; ×764.

the fronds being kept quite wet in the first instance by keeping the plants under a bell jar, and in the second case by submerging them. The species used were *Trichomanes radicans*, *T. crispum*, *T. rigidum*, *T. capillaceum*, *Hymenophyllum sericeum*, and *H. hirsutum*. The first of these was the only species influenced. Under bright diffuse light for 2 hours, about one-third of the chloroplasts had gone to the lateral walls, and illumination for 4 hours sent one-half of them there. The influence of full sunlight was nearly identical. When all of the above-named species were placed in total darkness for 20 hours, the chloroplasts were found in their normal positions on the outside walls.

These tests serve to indicate that intense illumination brings about a movement of the chloroplasts only in *T. radicans*. Since it is found only in heavily shaded habitats, and since species in which there is no responsive movement in strong light are found to have a portion of their chloroplasts on the lateral walls when the

surface is dry, it would appear that it is the dryness of the leaf surface rather than conditions of illumination that are responsible for the change of position of the chloroplasts.

Conclusions

The foregoing experiments have demonstrated that the filmy ferns may obtain water by any of three methods: root-absorption, leaf-absorption, and the absorption of atmospheric moisture by the leaves. By far the greatest mass of water intake is by leaf-absorption, root-absorption operating intermittently according to the wetness of the leaves. The high epiphytes are the only forms capable of availing themselves of atmospheric humidity, and the actual amounts of water thus obtained are small. The effect of a pronounced fall in humidity is to remove the water film from the leaves and to stop leaf-absorption; root-absorption is then taxed to a degree dependent on the lowness of the humidity and the duration of its lowness. Fig. 1 shows two drops in the humidity curve to below 70 per cent, neither of which lasted over 2 hrs., and it is probable that this trace, showing 4 hrs. of humidity below 70 per cent in the week, is representative of the average conditions of the floor of the rain forest.

When the surface of a leaf remains dry in a moist atmosphere, many, or even nearly all, of the chloroplasts will be found on the lateral walls of the cells. The duration of dryness necessary to bring this about varies from 3 or 4 hrs. in *Trichomanes rigidum* and other hygrophilous forms, to 8–10 hrs. in *Hymenophyllum polyanthos*. In the more hygrophilous species the removal is accompanied by a curling of the leaf, which is more a function of the humidity of the atmosphere than of surface dryness. If leaves are dried and suddenly placed in an atmosphere of 70 per cent humidity or less, the curling will take place before the movement of the chloroplasts. The movement appears to occur at times when there is no absorption of surface water taking place, but when there is a maintenance of the turgidity of the leaf by the movement into the leaf of root-absorbed water. The shifting of the chloroplasts appears, in other words, to be such as to place them opposite the walls through which the entry of water is going on.

When a gradual fall of humidity is experienced by surface-dry leaves, they assume withered shapes, and air bubbles appear in the cavities. If isolated leaves in this state are placed in a moist chamber, they will resume an appearance of turgidity within a few hours, and while the bubbles are still present in the sap. This false resumption of turgidity is therefore no more than the absorption of water vapor by the walls, and shows that the wetness of the walls rather than their distention by sap pressure is the cause of the turgidity of the leaves. The recovery of false turgidity is accompanied by considerable gains in weight, and these gains have already been shown to continue for several days. The absorption of atmospheric moisture is not great enough to replace the air bubbles in the cells when they have once appeared. Leaves of *Hymenophyllum polyanthos* with bubbles in the older cells have been kept for 5 days in a nearly saturated atmosphere without an appreciable diminution in the size or number of bubbles. The cells at the tip of the leaf and the tips of the terminal pinnae, which are richer in protoplasm, were at no time deprived of water sufficiently to have bubbles, and doubtless drew upon the supplies of water in the older cells.

The more hygrophilous species are not capable of withstanding a considerable loss of water from their sap cavities; while both *Hymenophyllum polyanthos* and *H. sericeum* have been found capable of withstanding very great losses. The extreme extent to which the lumen of the cells of *H. polyanthos* may be replaced by air is shown diagrammatically in fig. 8. The exposure of a dry leaf to sunshine for 30 min. or to very dry air (60–40 per cent) for an hour will suffice to bring about this condition. If the duration of the condition is not more than 1–3 hrs., the leaf will recover on being wet up, the chloroplasts (at first misplaced) will gradually (perhaps only after several days) resume their normal position, and the leaf will survive. A less degree of vacuolation of the leaf cells can be withstood for a longer time, but repeated attempts have shown it impossible to obtain any very exact measure of the behavior of leaves in this respect.

The physiological behavior of the Hymenophyllaceae in respect to their capacity for enduring the loss of water from the sap vacuoles

of their cells is similar to that of many xerophilous mosses, hepatics, selaginellas, and ferns. The filmy ferns are not capable of enduring as complete a removal of water as are the other archegoniates mentioned, but in view of the extremely hygrophilous character of most members of the family, it is sufficiently noteworthy that the few species which grow as high epiphytes in the Jamaican forests

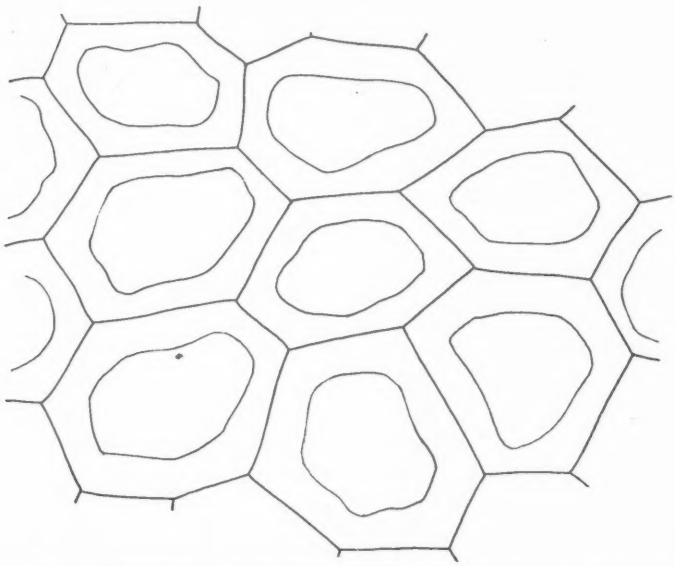

FIG. 8.—Diagram to show the maximum extent to which the sap cavities of the cells of *Hymenophyllum polyanthos* may be occupied by air bubbles in desiccated living leaves.

are capable of enduring as great water loss as they are. Whereas several families of flowering plants have contributed to the epiphytic flora of the rain forest species which are of xerophilous structure, the Hymenophyllaceae have contributed a small group of species the xerophily of which resides not at all in their structure, but in the capacity of the protoplasmic utricle to withstand the removal of the sap which is its source of water and nutrient salts.

Summary

1. The Hymenophyllaceae are most abundant in species and individuals at about 1525 m. altitude.

2. The Jamaican species differ in their relation to moisture conditions from the most pronounced hygrophily to a relative degree of drought resistance.

3. The differences of climate from floor to canopy in the rain forest determine the local distribution of the different types of Hymenophyllaceae.

4. The low water loss from surface-dry leaves in a very moist atmosphere can be met by root-absorption in all but the most hygrophilous forms.

5. The transpiration current moves when the leaves are wholly or partly surface-dry, but is at a standstill when the leaves are thoroughly wet.

6. All but the most drought-resistant epiphytic species of Hymenophyllaceae are capable of living for considerable periods as submerged aquatics.

7. The drought-resistant species are capable of absorbing atmospheric moisture when surface-dried, if kept in very moist air.

8. Continued desiccation results in the loss of the water of the sap cavity of all mature leaf cells, recovery depending on the duration of the desiccation.

9. The relatively xerophilous epiphytic Hymenophyllaceae owe their ability to resist drought to the capacity of the protoplasmic utricle of the leaf cells both to survive the replacing of the sap cavity by air and also to lose a rapidly diminishing amount of water on continued desiccation.

10. The Hymenophyllaceae (structurally and physiologically a very distinct group of ferns) have developed forms capable of growing in relatively dry situations through possession of an intracellular or functional xerophily, much less pronounced than that possessed by many mosses and selaginellas, but like it in kind.

THE DESERT LABORATORY
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A WAX SEAL METHOD FOR DETERMINING THE LOWER LIMIT OF AVAILABLE SOIL MOISTURE[1]

LYMAN J. BRIGGS AND H. L. SHANTZ

(WITH TWO FIGURES)

All soils upon which the plant cover has wilted through lack of water will still be found to contain moisture, varying in amount from less than 1 per cent in a coarse sand to 25 per cent or more in the heaviest clay soils. It is therefore highly important in all studies of the relationship of soil moisture to plant growth to recognize clearly that a simple statement of the moisture content of the soil gives no indication whatever of the amount of water actually available to the plant. To ascertain the amount of available soil moisture, it is necessary to determine the actual water content of the soil, and in addition the minimum to which the plant can reduce the soil moisture content. The difference between these two determinations represents the soil moisture that is actually available to the plant. The minimum to which a plant can reduce the water content of a soil is dependent upon a number of variable factors, and is somewhat lower than the moisture content corresponding to the wilting point. Practically speaking, the permanent wilting of the plant marks the cessation of growth, and in accordance with previous usage has been considered in the present paper as the criterion of non-availability. In a subsequent paper, we propose to compare the minimum of available moisture, as determined by the wilting point and by the death point, and to show to what extent this determination is affected by varying conditions of temperature, humidity, and light.

The method which we have employed consists essentially (1) in the use of an impervious pot, (2) in sealing over the soil surface in the pot with wax so as to prevent all evaporation from the soil, and (3) in keeping the soil mass at approximately constant temperature. Under these conditions the water remaining in the soil at the time of wilting is non-available to the plant.

[1] Published with the permission of the Secretary of Agriculture.

Essentials in determining non-available moisture

In determining the non-available moisture content of a soil, we have found that the following precautions are necessary:

1. The soil mass should be as uniform as possible, since the non-available moisture varies with the texture of the soil, and is consequently affected by stratification or other non-uniformity of the soil mass.

2. The soil should be brought to a uniform moisture content before being placed in the pots. Otherwise, small volumes of soil may remain dry and thus introduce an error in the final moisture determinations.

3. All loss of water from the soil should be prevented except that resulting from the transpiration of the plant. Otherwise, the surface soil may dry out below the minimum limit of available moisture, before the inner soil mass has reached this limit.

4. All sudden fluctuations in temperature must be avoided. Otherwise, condensation will occur on the inner walls of the pot as the result of distillation from the soil, due to the difference of temperature. This condensed water will be absorbed by the roots in contact with the inner walls of the pot, and the moisture content of the principal soil mass may thus be reduced below the minimum of available soil moisture.

Description of the method

In working out a practical method embodying the above requirements, which have not been fully complied with in the methods heretofore described, we have adopted the following procedure:

1. The air-dried soil is sifted through a 2 mm. screen to remove gravel and to insure greater uniformity. The soil, after sifting, is thoroughly mixed, special care being taken to avoid the separation of the fine and coarse particles. Variation in the amount of gravel and coarse sand in the different pots produces irregularities in the non-available moisture determinations, due to the fact that the coarse particles add to the weight of the soil without appreciably contributing to its water-holding properties.

In certain soils, notably those deficient in lime, it is best to add a small amount of calcium carbonate to the soil before planting, to insure the growth of the seeds.

2. The proper amount of water to be added to the air-dried soil is dependent upon the soil texture, varying from 5 per cent for sand to 30 per cent for clay. The amount to be used is best determined by adding water slowly from a graduate to a small weighed portion of soil until a condition of good tilth is reached. A heavy soil can be moistened without puddling by placing it on a slab or table in a cone-shaped pile, with a large crater in the top, into which the required amount of water is slowly poured. The crater is then filled with dry soil from the sides, and the whole mass is covered to prevent evaporation, and allowed to stand over night, or preferably longer. The soil is then thoroughly mixed, during which process it is sifted through a coarse screen ($\frac{1}{4}$ inch mesh). Any pellets of soil having more than their proportionate amount of water will be removed in this way. After mixing, the moist soil should be kept in a tight receptacle until ready for use.

Impervious pots of course must be used in order to prevent the soil in contact with the pots from drying out below the minimum of available soil moisture. We have found that ordinary straight-walled drinking glasses form very satisfactory pots for this work. During the process of filling the glasses, the soil is slightly compacted by jarring the bottom of the glass against the hand. Three to five seeds are planted in each pot, about 1 cm. in depth, after which the surface is smoothed and compacted slightly. The soil surface after planting should be about 1 cm. below the edge of the glass. It is sometimes advantageous to plant seeds which have just begun to germinate; this insures a uniform stand, and avoids excessive respiration below the wax seal.

3. In sealing the pots the wax is heated slightly above the melting point, and a sufficient amount is poured into the pot to cover the soil surface about 3 mm. in depth. The pot is rocked slightly so as to bring the wax into thorough contact with the inner walls of the pot, after which the excess wax is poured off. If the wax is at the proper temperature, this will give a perfect uniform seal over the entire surface. If the seal is not perfect, the process is repeated. The wax layer should be approximately 1 mm. in thickness, and should be in close contact with the soil. If the wax does not adhere to the soil surface, the pots should be resealed, since the plants may buckle under the wax cover if it is not adherent.

In the case of monocotyledons, we have found that the wax seal can best be added immediately after planting the seeds. On germination, these plants will grow readily through the wax, which forms a perfect seal around the stems (fig. 1). With dicotyledons it is advisable to keep the pots in a moist chamber, to reduce evaporation until the seedlings appear above the ground, when the wax seal can be applied without injury to the plants.

Even in the case of dicotyledons, this wax seal is often applied at the time of planting. This prevents the soil from drying out between the time of planting and complete germination. Plants which do not raise the cotyledons above the soil surface and those with very small seeds often push through the wax without breaking the seal. Other dicotyledons push their way through the wax cover without any difficulty, although it is necessary to reseal these pots after the seedlings are all up, especially in the case of plants with large cotyledons, such as the bean, squash, cucumber, etc.

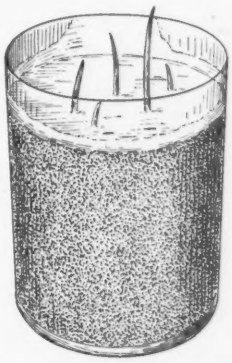

FIG. 1.—Showing the wax seal on the surface of the soil in the glass container with wheat seedlings growing through the seal; the wax was applied immediately after planting the seeds.

Aeration, when necessary, can readily be accomplished by making two small holes through the wax to the bottom of the pot on opposite sides. A glass tube drawn to a small opening and connected with a wash bottle is forced into one hole to supply moist air, and a similar glass tube is forced into the opposite opening and attached to an aspirator to withdraw the air from the pot. The wax forms a perfect seal around the glass tubes. In this way many pots can be aerated and the holes resealed with a hot wire in a comparatively short time.

The wax seal method is also particularly adapted to the study of transpiration, since all loss of water is avoided except through the plant tissues.

4. Serious fluctuations in temperature can be avoided by immersing the pots to within 5 mm. of the top in a tank, preferably one through which a small stream of tap water is constantly flowing.

In case this is not feasible, the pots can be immersed in a barrel or large tank of water, in which a constant circulation is maintained.

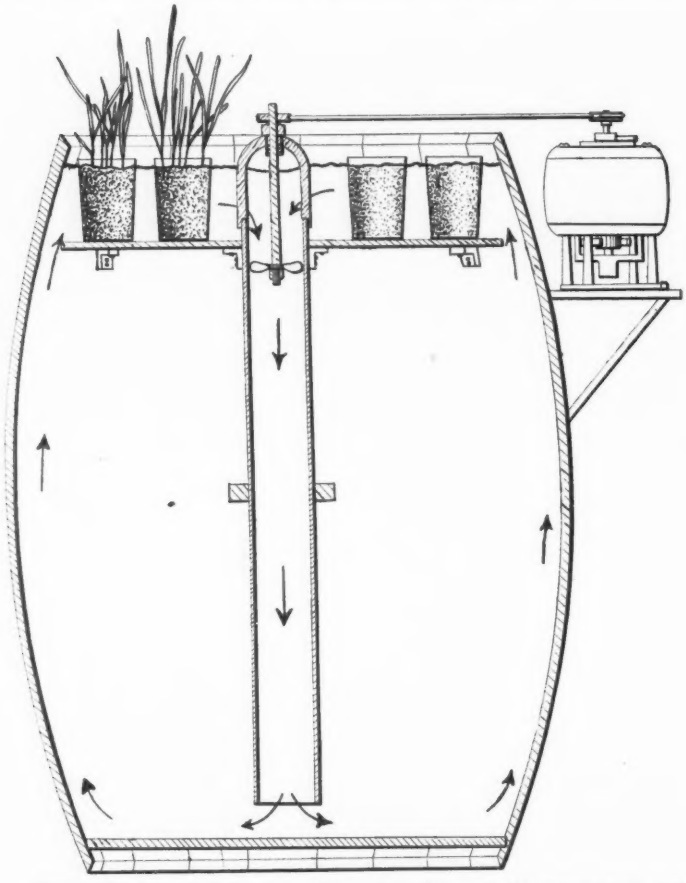

FIG. 2.—Showing tank for preventing sudden changes in the temperature of the soil used in non-available determinations; the propeller in the central tube causes a constant circulation of the water around the pots.

The most satisfactory form of stirring device that we have used consists of a small propeller in a tube (fig. 2). The upper end of the tube carries a yoke which supports the bearing of the propeller

shaft. The propeller is driven by a horizontal belt from a small vertical shaft motor mounted on a bracket at the top of the barrel. The lower end of the propeller tube extends nearly to the bottom of the barrel, while the upper end fits into the center of the solid shelf on which the pots rest. An annular space is provided between the shelf and the barrel. The operation of the stirrer causes a circulation downward through the central tube, upward along the walls of the barrel, and radially inward across the shelf and around the pots. While the temperature of even this large volume of water will vary somewhat during the day, these changes are very gradual, and are found to produce no detrimental effect. For the purpose, a simple arrangement of this kind is preferable to a more elaborate thermostat.

As soon as the plants in a pot show unmistakable signs of wilting, the water content of the soil is determined. The pot is inverted, and the soil mass removed intact by gently jarring the edge of the pot against the bench in the usual way. The lower two-thirds of the soil mass is taken for the moisture determination, since the roots do not usually develop so extensively in the upper portion. The moisture determination is based upon the loss of water taking place when the soil is dried to constant weight at 100° C., the percentage of moisture being based upon the dry weight of the soil.

Composition of the wax seal

For sealing the pots, we have tried paraffin, petrolatum, beeswax, and tallow in various proportions. Of these, we have found a wax composed of 80 per cent paraffin (melting point 45° C.) and 20 per cent petrolatum to be most satisfactory for use at ordinary temperatures, exact proportions not being important. This mixture melts at so low a temperature and has such low heat conductivity that it can be poured into a pot around the most delicate seedling without injury. This is an important point in the case of delicate dicotyledons. On cooling, this wax adheres well to the glass and to the soil, forming a perfect seal. Other mixtures, notably those containing beeswax, show a decided tendency to separate from the glass on cooling, necessitating resealing the edges with a hot iron.

None of the substances mentioned give good results when used alone. Paraffin (45°) stretches, petrolatum creeps, and beeswax, tallow, and the higher paraffins crack. Except in the case of the soft paraffin, which stretches, the plants show no difficulty in penetrating the wax cover, even when a wax as hard as that used in making the ordinary commercial phonograph records is used as a seal.

During the winter in the greenhouse the paraffin-petrolatum mixture gives excellent results even when left in direct sunlight. However, during the warm portion of the year direct sunlight is likely to melt this wax, and in this way break the seal and cause damage to the plants, due to the wax creeping over the plant surface. The beeswax mixtures have proven best during warm weather. A mixture of 10–30 per cent beef tallow with beeswax, or of 8–12 per cent of petrolatum with beeswax, has proven an excellent material both in greenhouse and for out-of-door work.

Modelling clay has also been used to seal the pots, but it is not so easily applied as the wax, and is not suitable for use with delicate seedlings.

Experimental error

In determining the non-available moisture in a given soil, some variation will be found in the results obtained from the individual pots. This variation is probably due in part to the lack of uniformity of the soil in the different pots, but mainly to the fact that in some pots the roots are distributed through the soil mass much more uniformly than in others. When the root distribution is defective, the mean distance through which the soil moisture must move through capillary action is relatively greater. Since capillary movement is very slow in soils that are approaching their non-available moisture content, the portion of the soil not penetrated by roots would have a somewhat higher moisture content. The non-available moisture determination in the case of an imperfect root distribution would consequently be somewhat too high. On the other hand, errors arising from the distillation of water to the walls of the pot would result in giving a non-available determination below the true value.

Some uncertainty also arises in connection with the determina-

tion of the wilting point. Plants often wilt down during the day and recover during the night. The wilting of a plant in the hot part of the day is therefore no indication that moisture is not available. We have consequently considered a wilted condition in the morning as proof that the moisture content had been reduced to the point of non-availability. Check determinations were repeat-

TABLE I

INDIVIDUAL POT MEASUREMENTS OF NON-AVAILABLE MOISTURE FOR KUBANKA WHEAT IN THREE SOIL TYPES

	Fine sand per cent	Fine sandy loam per cent	Clay loam per cent
	2.6	...	16.9
	2.1	...	16.8
	2.7	...	16.4
	2.8	9.7	16.2
	2.6	9.3	15.5
	2.7	9.9	15.7
	2.7	10.1	17.3
	2.6	9.7	16.7
	2.5	9.4	15.6
	2.6	9.6	16.0
	2.4	9.3	16.0
	2.7	9.4	16.2
	2.6	9.8	16.3
	2.5	9.3	16.3
	2.7	9.7	16.7
	2.7	9.4	16.3
Mean	2.59	9.66	16.3
Probable error of mean	±0.03	±0.05	±0.09
Probable error of single observation	±0.11	±0.18	±0.34

edly made by placing the pots containing wilted plants under a bell jar in nearly saturated air. These plants were unable to recover their turgidity. Since the wilting point is influenced to some extent by the temperature and humidity of the air of the plant house, these conditions should be determined and kept as uniform as possible during the growth of the plants.

The degree of accuracy which may reasonably be expected by the wax seal method is shown by the series of determinations made with Kubanka wheat shown in table I, which gives the percentage of non-available moisture found in each pot for three types of soil. The plants were grown in an ordinary plant house. The average temperature was about 70° F., and the relative humidity

about 85 per cent. The mechanical composition of the soils employed is shown in table II.

Table I shows the arithmetical mean of each series of determinations, together with the probable error of the mean and the probable error of a single observation. The term "probable error" is used in its usual mathematical sense, that is to say, in the case of the series of determinations in sand, the chances are even if the series were repeated with the same soil that the mean would lie between the values 2.56 and 2.62; and if the experiment were repeated with a single pot, the chances are even that the non-available moisture in this pot would fall between 2.48 and 2.70. The prob-

TABLE II

MECHANICAL ANALYSES OF SOIL SAMPLES USED IN THE DETERMINATIONS GIVEN IN TABLE I*

	Fine gravel 2–1 mm.	Coarse sand 1–0.5 mm.	Medium sand 0.5–0.25 mm.	Fine sand 0.25–0.1 mm.	Very fine sand 0.1–0.05 mm.	Silt 0.05–0.005 mm.	Clay 0.005–0 mm.
	per cent	per cent	per cent	per cent	per cent	per cent	per cent
Fine sand	0.4	9.8	17.0	50.1	14.3	4.7	3.9
Fine sandy loam	0.1	1.5	1.2	10.2	49.6	30.2	6.9
Clay loam	0.1	2.3	2.0	6.6	13.9	52.6	22.0

* Mechanical analyses made by the Bureau of Soils.

able error of the mean is about 0.005, and that of the single observation 0.02 of the actual non-available determination in the loam and clay soils, while the corresponding probable error is about twice as great in sand. It appears, therefore, that while there is considerable variation in individual pots, the mean of a suitable series represents the non-available moisture content of a given soil with an accuracy fully comparable with the accuracy with which the soil itself can be defined through its physical properties.

Summary

All soils upon which the plant cover has wilted through lack of water will still be found to contain moisture, varying in amount from less than 1 per cent in coarse sands to 25 per cent in the heaviest clays, and even more in the peat soils. The available water in the soil at any time is represented by the difference between the actual water and the non-available portion. It is consequently

essential in any critical study of the relation of plant growth to soil moisture to be able to determine for any soil the maximum amount of non-available moisture.

In determining the non-available moisture, the permanent wilting of the plant has been taken as the criterion of non-availability. In making such determinations the following precautions are necessary:

1. The soil used should be as uniform as possible.

2. The soil should be brought to a uniform water content before being used.

3. All loss of water should be prevented except that due to the transpiration of the plant.

4. All sudden fluctuations in soil temperature should be avoided.

5. It should be definitely ascertained that the plant cannot recover turgidity without additional moisture being supplied.

The method which we have employed consists in growing the plants in a small glass pot, evaporation from the soil surface being prevented by means of a seal of wax which is melted and flowed over the soil surface. In the case of monocotyledons, this wax seal can be applied immediately after planting the seeds, and the seedlings will grow readily through the wax, forming a perfect seal around the stems. In the case of dicotyledons, the wax, which is usually a mixture of paraffin and vaseline having a low melting point and low heat conductivity, can be melted and flowed around the stems of the seedlings without injury. During growth, the pots are kept immersed in a water bath to avoid condensation of the soil moisture on the pot walls.

The probable error of the mean of the determinations from 12 pots or more does not usually exceed 0.1 per cent of actual soil moisture, which is fully comparable to the accuracy with which the soil itself can be defined through its physical properties.

The wax seal method is also particularly adapted to the study of transpiration, since all loss of water is avoided except that taking place through the plant.

Bureau of Plant Industry
Washington, D.C.

THE TEMPERATURE COEFFICIENT OF THE DURATION OF LIFE OF BARLEY GRAINS

T. HARPER GOODSPEED

LOEB[1] believes that the chemical reactions underlying the development of organisms differ widely from those that bring about natural death. This author has found, for sea urchin eggs, the temperature coefficient of duration of life to lie between 500 and 1000 for a rise of temperature of 10° C., while that of development was 2.86 for a similar temperature interval. This latter figure is identical with that previously calculated by PETER[2] from the results obtained by HERTWIG[3] in experiments upon the effect of temperature on the rate of development of frogs' eggs. MOORE,[4] using *Tubularia crocea*, states that the temperature coefficient of life duration in this hydroid was about 1000 for a rise of temperature of 10° C., and that the average temperature coefficient for the process of regeneration was 3.4 for a 10° C. interval. The influence of temperature upon the development of plants has been given some attention; but the results, as given in the literature, with a few exceptions yield no accurate conclusions. The obvious effect upon reaction velocities of even slight variations in the temperature, when the whole temperature range employed lies well within that which is normal for the subjects investigated, is the cause assigned for the inaccuracy of the results obtained. However, the careful experiments of CLAUSEN[5] upon the influence of temperature on the excretion of carbon dioxide by bean germs, wheat germs, and syringa buds have been widely recognized, and set a criterion of accuracy and technic for the investigations of plant physiologists along these general lines.

It was suggested to me that a temperature coefficient for the

[1] LOEB, JACQUES, Archiv. Ges. Physiol. **124**:411.

[2] PETER, KARL, Archiv. Entw.-Mech. **20**:130.

[3] HERTWIG, O., Archiv. Mikr. Anat. u. Entw.-Gesch. **51**:893.

[4] MOORE, A. R., Archiv. Entw.-Mech. **29**:145, 287.

[5] CLAUSEN, Landwirtschaftliche Jahrbücher **19**:893.

duration of life of seeds might yield interesting results if the determinations could be made sufficiently accurate. Experiments were accordingly begun September 1, 1910, and continued for some three months. It seemed to me that the use of barley in such an experiment would possibly yield results of the most scientific interest, since, from the observations of KIRCHHOFF[6] to the comprehensive researches of BROWN and MORRIS[7] and others, this member of the Gramineae has been the subject of much investigation.

The material was obtained from the American Hop and Barley Company, grown at their ranches in Butte County, California, and harvested during August 1910. The grain was given no specific name by the company, but is known in the trade as malt or brewing barley. Through the courtesy of the company, a quantity of their best grain used for exhibition purposes was at my disposal. It was characterized by them as being a trifle under the maximum weight, but uniform throughout and of the best color.

Previous to every temperature determination, the inferior palea of each barley grain was carefully removed, and 50 seeds were soaked in tap water for one hour. The material thus prepared was used within ten minutes after being removed from the water. It was judged that the removal of the outer seed coat would obviate the source of error that might otherwise be introduced through the different degrees of resistance to penetration offered by the protective coverings. By soaking previous to the experiments it was hoped that sufficient water would enter the tissues of the grain to affect a more rapid adjustment of the temperatures within and without the seed when placed in the water bath. The use of more than 50 seeds for each determination was considered to be unnecessary, inasmuch as control experiments including over 2000 seeds gave only 0.4 per cent as the percentage that would not germinate under normal conditions. This source of error may be considered negligible.

Two methods were employed for maintaining a constant temperature. In the first a double water bath heated by a Bunsen

[6] KIRCHHOFF, SCHWEIG'S Journal **14**:389. 1815.

[7] BROWN and MORRIS, Jour. Chem. Soc. **57**:458.

burner flame was used, the regulation of the temperature being made automatic by the use of a mercury thermo-regulator. A finger bowl containing 100 cc. of tap water stood upon the water bath, and the seeds, lying upon a square of loosely woven cotton cloth, were placed within it. By the use of such a container for the seeds, it was possible to remove all of the material at exactly the same moment. In the second method an electric incubator, within which stood a beaker containing 100 cc. of water, was found to give excellent results. An additional stove attachment and an electric regulator on the apparatus made it possible to maintain high and constant temperatures. When the temperature in the beaker had been kept constant at the desired point for an hour, the seeds were dropped into the water and could be taken out at the end of the time intervals almost as rapidly as in the former method. The whole temperature range given in the table below was covered according to the second method, while the effect of temperatures between 60° and 70° C. was investigated according to the first. The variations in temperature amounted to 0°.2 C. for the temperatures above 60° C., and 0°.3 C. for all temperatures below and including 60° C. The time during which these variations lasted, however, was relatively so short that this source of error may be disregarded.

For observing the progress of germination the seeds were placed upon moist filter paper so arranged in a finger bowl containing about 20 cc. of water that the surface of the paper was continually moist without any appreciable amount of water surrounding the seeds. In many cases the paper was perforated and the seeds, proximal end downward, were lightly pushed into the openings. A difficulty was encountered in connection with the molds *Rhizopus nigricans* and *Penicillium crustaceum*, which usually attacked the seeds on the third or fourth day. Any seeds that were evidently dead and decomposing were at once discarded as soon as the mold appeared, and any others affected but showing signs of germination were carefully watched and kept free from mold by wiping with sterilized lens paper. In all cases the material was kept at room temperature and in partial darkness.

The criterion of complete development was the appearance of the green shoot above the plumule sheath or the formation of roots from the swollen radical extremity. The normal stages observed in the germination of barley are, first, the protrusion of the calyptrogen and a rapid development of the three primary roots therefrom, and second, the appearance, at a shortly later period, of the plumule sheath, within which the leaves of the plumule are contained. The effect of all temperatures above 64°C. for the time intervals mentioned below was to inhibit in every case the normal development of the radicle. Development appeared in the plumule after intervals varying from 15 to 30 hours, and continued slowly until at the end of two days the green shoot began to show. From 2 to 3 days later adventitious roots began to take form from the basal portion of the plumule sheath, probably from the point of origin of the procambium strands that enter the scutellum, leaves, and radicle. The germination and subsequent development of certain seeds subjected to a temperature of 66° C. for 5 minutes was observed through a period of five weeks, and it was noted that after the appearance of the adventitious roots growth proceeded rapidly, and at the end of this period these plants compared favorably with those germinating normally and growing for an equal length of time.

Temperature Centigrade	Duration of life	Temperature coefficient for 1° C.
70	$1\frac{1}{2}$–2	
69	2– $2\frac{3}{4}$	1.3
68	3– 5	1.7
67	4– 5	1.1
66	5– 6	1.2
65	6– 8	1.3
64	7– 9	1.1
63	10–12	1.4
62	11–12	1.0
61	15–16	1.3
60	18–19	1.2
59	21–24	1.2
58	24–26	1.1
57	32–35	1.3
56	42–47	1.3
55	65–70	1.5
Average temp. coefficient 1.27		

The preceding table expresses the results of some 300 separate determinations in which over 15,000 seeds were used. Each time interval was repeatedly verified, and since in some cases exactly corresponding results could not be obtained, an average was in such cases taken. The duration of life of the seeds was taken to be the time in minutes for which a given temperature must act in order to inhibit the subsequent growth of all the seeds when placed under the conditions above described.

The temperature coefficient of the duration of life of barley grains has been determined for the temperatures 55°–70° C., inclusive, and has been found to be about 11 for a temperature interval of 10°. This is of the order of magnitude demanded by the law of VAN'T HOFF and ARRHENIUS for the temperature coefficient of a chemical reaction, but is much less than the temperature coefficient of duration of life of sea urchin eggs as determined by LOEB.

I wish to acknowledge my indebtedness to Professor W. A. SETCHELL for his many helpful suggestions and criticisms, and to A. R. MOORE, whose continued interest and assistance have made this paper possible.

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BRIEFER ARTICLES

NOTES ON FUNARIA HYGROMETRICA

(WITH FIVE FIGURES)

It is usually assumed by most authors of botanical textbooks that *Funaria* is dioecious. CAMPBELL[1] says that it is "strictly dioecious." BOODLE[2] showed that while in general the sex organs are borne on separate plants, occasionally archegonial heads arise as branches of a main axis which is terminated by an antheridial head. HOLFERTY[3] claimed that in *Mnium* the egg and ventral canal cell may sometimes be the same size. In an undetermined species of *Mnium*, COKER[4] found two distinct eggs, with their ventral canal cells, at the base of and in direct line with the single row of neck canal cells.

While examining large quantities of *Funaria hygrometrica*, two or three well developed antheridia and the same number of quite mature archegonia were repeatedly found in the same head, which was usually conspicuous on account of its size. Also in these heads antheridia with a bulbous basal and a tapering apical region, resembling quite closely the general form of a short-necked archegonium, were not uncommon.

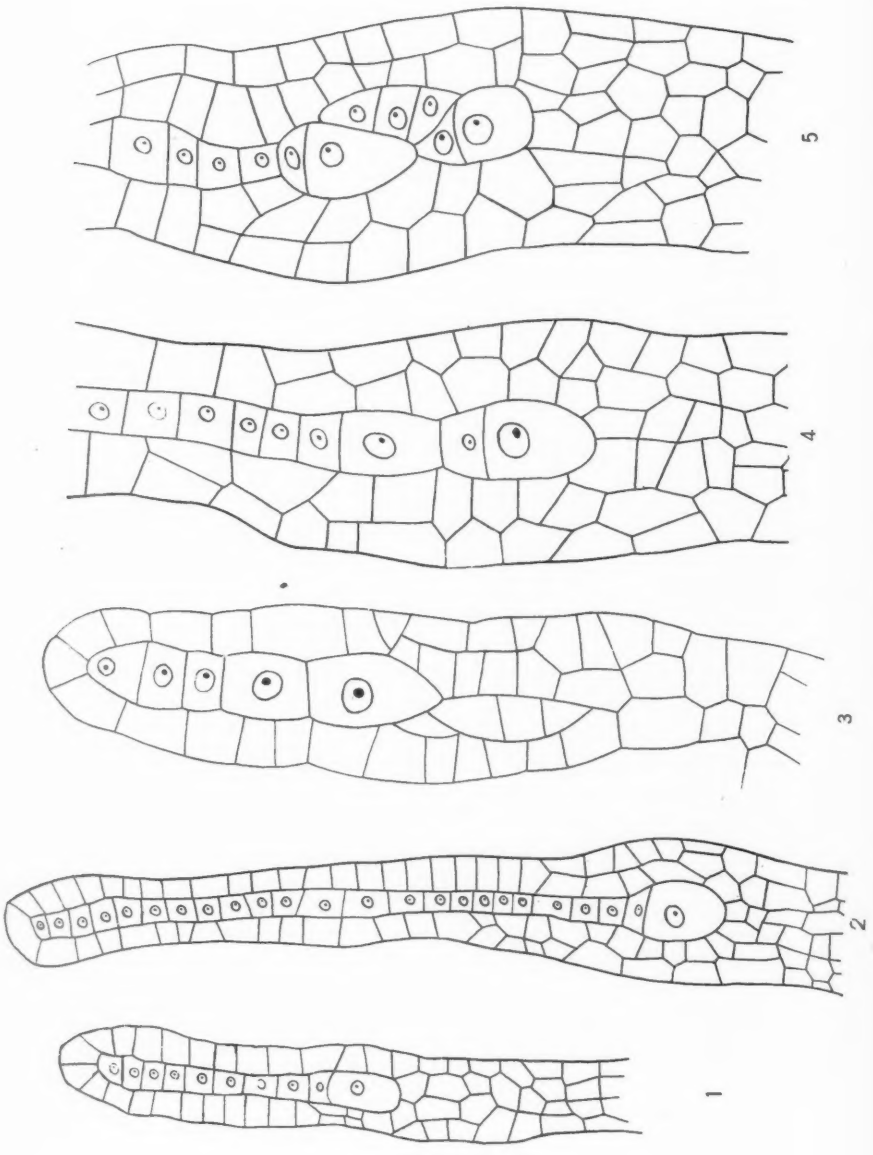
The archegonia of *Funaria* usually have 8–12 neck canal cells. An ordinary archegonium with 8 neck canal cells and the usual long stalk is shown in fig. 1. Fig. 2 shows an extremely long-necked archegonium, which had 22 neck canal cells and a relatively short stalk. This archegonium was found in a head which also bore 5 antheridia. Fig. 3 shows an archegonium in which two eggs will finally develop; the ventral canal cells have not yet been cut off. Fig. 4 illustrates the presence of two eggs and their ventral canal cells. Fig. 5 shows an archegonium having 2 eggs, each of which is definitely related to its own row of neck canal cells. The three neck canal cells belonging to the lower egg have been pushed aside by the upper egg.

[1] CAMBPELL, D. H., Mosses and Ferns, 1905. p. 195.

[2] BOODLE, L. A., The monoecism of *Funaria hygrometrica* Sibth. Annals of Botany **20**:293–299. *figs. 2*. 1906.

[3] HOLFERTY, G. M., The development of the archegonium of *Mnium cuspidatum*. BOT. GAZETTE **37**:116–126. *pls. 5, 6*. 1904.

[4] COKER, W. C., Selected notes. BOT. GAZETTE **35**:135–138. 1903.


5
4
3
2
1

It seems that the occasional occurrence of monoecious heads and also of more than one egg in an archegonium may indicate reversions to a more primitive ancestral type.—JENNIE M. SPEER, *The University of Chicago.*

A PORTABLE, ADJUSTABLE CAMERA STAND

(WITH THREE FIGURES)

Occasion frequently arises when the scientific worker, whether in the field, at his station, in the office, or in the laboratory, needs to use the camera vertically, or at various angles between the vertical and the horizontal. The ordinary tripod does not admit of such adjustment unless special lugs are provided in the camera box. With the writer the need has often arisen for some handy method of using his camera, whereby he might photograph objects that must be kept in a horizontal position, or, in the field, where the best results require an angular view. On this account the stand shown in the accompanying photographs was devised and used with perfect success and great saving of time.

FIG. 1

The stand is attached to any tripod by means of the standard tripod screw, and by a similar screw the camera is in turn attached to the adjustable stand as shown in fig. 2. In actual operation the tripod is set firmly with the legs spread out pretty well to give rigidity, and to allow plenty of space for the bed of the adjustable stand between any two of the tripod legs in the case of vertical work. The stand is then attached to the tripod and turned about until the bed (*b*, fig. 2) points in a direction exactly between

two of the legs. The camera is then screwed in place as shown in all the illustrations. All that is then necessary, supposing the stand has been placed directly over the object to be photographed, is to adjust the camera at the proper distance from the object by sliding

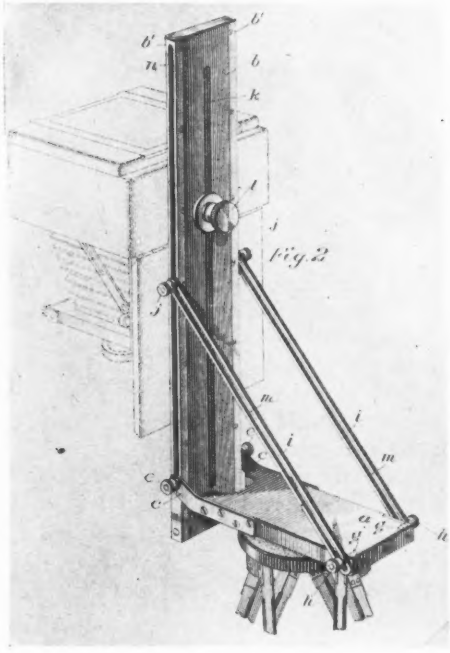


FIG. 2

it up or down the bed of the stand by means of the slot (*k*, fig. 2). The bed of the stand itself may be lowered or raised by means of the groove (*n*, fig. 2) and the binding screws (*j*, *j*, *c*, *c*). Fig. 1 shows the stand adjusted so that the camera shall be quite low, for use when objects on the ground are to be photographed on a large scale. Fig. 2 shows the stand adjusted for average vertical work; fig. 3 with the camera at an angle for photographing a plant or other object at about the same angle as it is usually viewed by a person standing near it. By reversing the camera, tall objects, such as portions of a tree, may be photographed.

The stand offers a long rigid base for quite heavy cameras and is admirably adapted for use with long-focus cameras; it may be folded compactly with the tripod or be packed in a suitcase. It is equally useful in the office and laboratory, where objects may be placed on some support, such as plate glass, to be photographed.

FIG. 3

The chief objection to any other device the writer has seen is that the tripod itself must be readjusted, always an awkward and tedious process. With this stand only the camera has to be moved to and fro on the bed to get the proper adjustment after the tripod has been set. —HARRY B. SHAW, *Bureau of Plant Industry, Washington, D.C.*

HOMOTHALLIC CONJUGATION IN RHIZOPUS

(WITH ONE FIGURE)

A single case of homothallic conjugation in *Rhizopus nigricans* has recently been observed at the Hull Botanical Laboratory. The

hypha had curved, and suspensors had developed on opposite sides of the coil (fig. 1). The appearance of the remnants of the wall between the gametangia showed that conjugation had taken place. While investigators have disputed Dr. BLAKESLEE's results that plus and minus strains are necessary for sexual reproduction, so far as we know the observation of conjugation between two closely approximate parts of the same hypha has not entered into the discussion. This peculiar

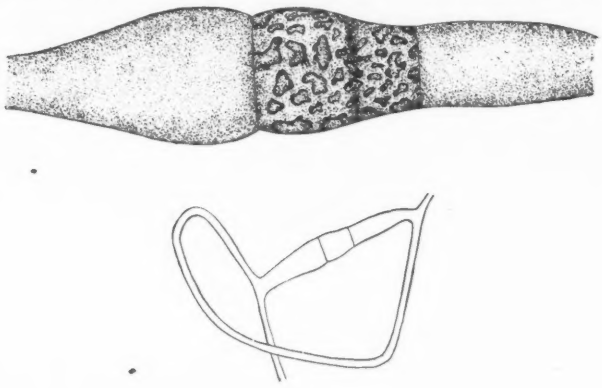


FIG. 1

mode of conjugation was accidentally found in some material grown from spores obtained from J. I. HAMAKER of Randolph-Macon Woman's College of Virginia. The culture was grown on bread moistened with a solution of grape sugar, and zygospore-formation was unusually abundant. Dr. BLAKESLEE in his article in the BOTANICAL GAZETTE of June 1907 admits the possibility that a homothallic race may occur in a species normally heterothallic; and the case just cited substantiates that possibility.—FLORENCE A. MCCORMICK, *The University of Chicago.*

PISTILLODY OF STAMENS IN HYPERICUM NUDIFLORUM

A plant of *Hypericum nudiflorum* Michx. cultivated at the Arnold Arboretum and in full bloom during the first week of October, while another plant of the same species had almost mature fruits, presented a very good example of pistillody of stamens. The inflorescence and the flowers did not at the first glance show any deviation from the normal except that the regular arrangement of the stamens seemed somewhat disturbed, but a closer examination revealed the presence between the

pistil and the stamens of a number of peculiar irregularly shaped bodies representing apparently deformed carpels. These deformed carpels or pistillodes, as they may be called, were present in each flower of the whole plant, which had about eight stems, each terminated by a many-flowered cyme. The number of the pistillodes in each flower varied from three to about ten, differing in size and development. Most of them were boat-shaped, distinctly curved, and with the concave side directed toward the normal pistil; on both margins, except near the base and near the apex, they bore numerous ovules partly hidden in the concavity and partly exposed; on each side, directly below the apex, a yellow oblong spot was noticeable, which apparently represented the rudimentary anther cells, while the variously shaped apex itself usually showed a greenish color like the upper part of the style, and represented apparently the rudimentary stigma. Sometimes two of the pistillodes were more or less united at the base, and in a few cases pistillodes were divided at the apex; in one case I found one part of the divided apex representing a rudimentary anther and the other half a rudimentary stigma. Pistillodes with fertile anthers were not common; in a few cases the dilated but scarcely concave filament bore a few ovules on one side of the filament only and an anther larger than the normal, or the filament was only dilated without ovules. In some of the smaller pistillodes a few of the ovules, particularly toward the apex, were changed into greenish elongated appendages, which usually, by a peculiar bend, still preserved the anatropous character of the normal ovule. This phyllody of ovules is not at all uncommon with exposed ovules. All other parts of the flower (calyx, petals, stamens, except the few deformed ones, and pistils) were perfectly normal in all the flowers.

The teratological facts here described seemed interesting enough to be put on record, particularly as apparently no other similar case has been reported in the genus *Hypericum*. PENZIG[5] records under *Hypericum* only cases of adventive buds, deviation from the ordinary number in the floral whorls, decrease of size in leaves, and one case of apostasis in the calyx. This tends to show that *Hypericum* has little tendency to form abnormalities, and may serve as an excuse for the publication of the present case. Specimens are preserved in the herbarium of the Arnold Arboretum.—ALFRED REHDER, *Arnold Arboretum*.

[5] Pflanzen-Teratologie 1:308, 309.

CURRENT LITERATURE

BOOK REVIEWS

Ecology of Isle Royale

Isle Royale, Lake Superior, is a strategic point for ecological and biogeographical investigation for several reasons. It is situated in the boundary zone between two great life areas, the northeastern conifer forest region, and the eastern deciduous forest region. The isolation of the island from the mainland throughout its postglacial history has produced ideal conditions for the study of certain phases of plant and animal migration. Isolation has also resulted in unusual freedom from disturbing factors such as fire. Finally, the occurrence of certain forms far out of their ordinary range suggests opportunity for valuable floristic and faunistic investigation. The Michigan Biological Survey made a fortunate choice of a field of study when it sent the University Museum party to Isle Royale in the summer of 1905. During 1904 a similar expedition, including three of the same members, worked on the island for a few days, after spending some weeks in the Porcupine Mountains of the Northern Peninsula.[1]

The 1905 expedition was under the leadership of Dr. C. C. ADAMS, now of the University of Illinois, and about half of the report[2] was written by him. The prime object was ecological investigation from a dynamic standpoint. In nearly every phase of the work the successional relations of the biota were emphasized. In connection with this study the forms were listed and collections made, and most of the resulting catalogues are doubtless as complete as the limited time permitted.

The first thing that strikes one in glancing over the volume is that the report is dominantly, almost exclusively, a zoological study, only 31 out of 422 pages being devoted to the vegetation. We are left absolutely without a clear idea of the vegetation of the island—its aspect and relations—in spite of the fact that the animal successions are entirely dependent upon those of the vegetation. It should be said, however, that everywhere in the discussion this necessary relation is fully recognized. The trouble is that without an adequate discussion of the vegetation as a foundation it is impossible for a

[1] An ecological survey of northern Michigan. Prepared under the direction of C. C. ADAMS. Lansing. 1906.

[2] ADAMS, C. C., An ecological survey of Isle Royale, Lake Superior. A report from the University of Michigan Museum published by the State Biological Survey as a part of the Report of the Geological Survey for 1908. pp. xiv+468. *figs. 63*. Lansing, Mich. 1909.

stranger to the region to gain a true conception of the interrelations of the whole biotic complex.

The report consists of two parts, including respectively ecological papers and annotated lists. Under part I we find the following: (1) Isle Royale as a biotic environment, C. C. ADAMS; (2) The ecological relations of the invertebrate fauna of Isle Royale, H. A. GLEASON; (3) The ecological distribution of the birds of Isle Royale, OTTO MCCREARY; (4) Fall migration of birds at Washington Harbor, Isle Royale, MAX M. PEET; (5) The ecological succession of birds, C. C. ADAMS; (6) The Coleoptera of Isle Royale, and their relation to the North American centers of dispersal, C. C. ADAMS. Part II includes annotated lists as follows: Notes on the vegetation of Isle Royale, and annotated lists of plants, W. P. HOLT; and various zoological lists prepared by members of the expedition and specialists.

The papers that treat directly or incidentally of the vegetation are nos. 1 and 2 of part I and HOLT's annotated list. The last, the only part directly concerned with the vegetation, comprises ten pages of ecological notes, followed by an annotated list of lichens, mosses, ferns, and seed plants. The total number of species listed is 364. That this list is very incomplete is shown by the fact that a number of species are mentioned in other parts of the report as occurring commonly, which do not appear at all in the catalogue. The very brief discussion of the vegetation that precedes the list is totally inadequate.

In the introductory paper of the report, "Isle Royale as a biotic environment" by ADAMS, there is much of interest and value to plant ecologists. The writer discusses the geologic history of the island, the climate, and the development of the habitats. The probable effect of the lake storms and surface currents in determining the composition of the flora and fauna is also treated in an interesting way.

GLEASON in his treatment of the invertebrates makes many incidental but valuable observations upon the plant successions. The brief summary with its appended generalized diagram showing the courses of the successions is the most valuable contribution to the plant ecology of the island to be found in the report.

Every ecologist, whether working with plants or animals, should read ADAMS' papers on the birds and the Coleoptera.

The report as a whole is an exceedingly valuable contribution, and Dr. ADAMS deserves great credit for carrying the work through to completion under conditions of very great difficulty. Upon such detailed studies of strategic localities will be built our future completer knowledge of biogeography. It is to be hoped that many similar expeditions may be carried out in various parts of the continent before further settlement and exploitation seriously interfere with natural conditions. It is also to be hoped that in all such studies the vegetation be given its full share of attention.—WILLIAM S. COOPER.

MINOR NOTICES

Lodgepole burn forests.—The Forest Service has recently issued a bulletin which should be of great interest to all ecologists. Dr. F. E. CLEMENTS,[3] working as collaborator, has made a study of the forests of lodgepole pine in the vicinity of Long's Peak, Colorado. He finds that the lodgepole forests in that region are invariably related to forest fires, since the tree reproduces abundantly only under the conditions initiated by such events.

By a determination of the ages of the oldest plants, principally lodgepoles, which have come into the given locality since the fire, and by study of fire scars upon the trunks, he sets the date of the fire and determines the extent of country affected by it. In this way he has discovered the dates and determined the extents of many fires of the past two centuries, with considerable accuracy in the case of the recent ones, with less accuracy in the case of the less recent. Eight fires were found to have affected the region during the nineteenth century, and the areas covered by several of them overlap. There were four fires during the eighteenth century and a probable one in 1676. The accuracy with which the dates may be determined is due to the fact that abundant reproduction of lodgepole occurs the first year after the fire, and the majority of the trees are therefore even-aged to the year.

A study of the life history of the species follows, in which is found the explanation of the particular type of forest which the lodgepole pine produces. Immediate and abundant reproduction is favored by fire because (1) it causes the opening of many cones at once without damaging the seed; (2) it brings about the temporary disappearance of rodents, which ordinarily consume immense quantities of seed; (3) abundant light is provided, a necessity for reproduction and growth in this species; (4) cover competition is destroyed.

Finally, the future development and treatment of lodgepole forests are discussed. If fire is kept out, the lodgepole forest zone will be gradually narrowed and ultimately crowded out of existence by encroachment of Douglas fir from below and of Engelmann spruce and subalpine fir from above, owing to the much greater tolerance of shade which these species possess. In order to produce a new crop of lodgepole, clear cutting of the forest will be necessary, followed by thorough burning. Mere cutting without fire does not produce the requisite conditions.—WILLIAM S. COOPER.

NOTES FOR STUDENTS

Alcoholic fermentation.—Important contributions to our knowledge of the fermentation of sugar have been made by HARDEN and YOUNG, and by IWANOFF, in their experiments on the action of phosphates in alcoholic fermentation. Although these investigators agree in the main, their views differ as to the details of the reactions involved in the fermentation of sugar in the presence

[3] CLEMENTS, F. E., The life history of lodgepole burn forests. U.S. Dept. Agri., Forest Service Bulletin 79. pp. 56. *pls.* 6. *fig.* 1. 1909.

of phosphates. For a clearer understanding of a number of recent papers on the subject by these writers, their views may be outlined briefly here.

The view of HARDEN and YOUNG, as expressed in a number of former papers, on the manner in which the addition of phosphates to a fermenting mixture of yeast juice and sugar causes an increased evolution of carbon dioxid, is derived from the following observations. When phosphates are added to a fermenting mixture of glucose and yeast juice, the amount of carbon dioxid evolved from the fermenting mixture is greatly increased. The extra carbon dioxid is all given off during an initial period of accelerated fermentation, after which the rate of evolution decreases and continues at a uniform rate. During the initial period of fermentation, the phosphates enter into combination with the sugar in a form not precipitable by ammoniacal magnesium citrate. During the second or uniform period of fermentation, the phosphates are again set free. The carbon dioxid given off during the initial period is chemically equivalent to the amount of phosphate added. These facts are formulated in the following equations.

$$\text{I.}\quad 2C_6H_{12}O_6 + 2R_2HPO_4 = 2CO_2 + 2C_2H_6O + 2H_2O + C_6H_{10}O_4(PO_4R_2)_2$$

$$\text{II.}\quad C_6H_{10}O_4(PO_4R_2)_2 + 2H_2O = C_6H_{12}O_6 + 2R_2HPO_4$$

According to this view, the phosphate combines with the sugar to form a hexose-phosphate. This reaction gives the extra carbon dioxid evolved during the initial period after the addition of a phosphate, while the rate of the second reaction determines the steady rate of fermentation at which the simple sugars are fermented by yeast juice without the addition of phosphates.

The view of IWANOFF differs from the foregoing chiefly in the following details. The phospho-organic compound formed in a mixture of sugar, zymin, or "Hefanol" and a phosphate is a triose-phosphate and not a hexose-phosphate. The formation of the triose-phosphate is not necessarily accompanied by the evolution of carbon dioxid, because the combination takes place also when a phosphate is added to the filtrate of a sugar solution which has been fermented by zymin. Therefore, the combination may take place without the accompaniment of fermentation or the evolution of carbon dioxid.

Further evidence in support of his interpretation is given by IWANOFF in a recent paper.[4] The main facts and conclusions of this paper may be stated briefly, without going into the experiments upon which they are based. It is found that the filtrate of a mixture of zymin and saccharose in water fermented one day is capable of combining with phosphates, but that this power of combination is lost when the filtrate is heated. The sugar which can be in part liberated from the phospho-organic compound is not fermentable by living yeast. Further, "Hefanol" washed with water will ferment the phospho-organic compound (triose-phosphate of the author), but not glucose, even after the addition of phosphate.

[4] IWANOFF, S., Ueber die Bildung der phosphororganischen Verbindungen und ihre Rolle bei der Zymasegärung. Centralbl. Bakt. II. **24**:1–12. 1909.

From these facts the following conclusions are drawn. First, the combination of sugar and phosphates is effected by a soluble enzyme to which the author gives the name "synthease." Second, if the phospho-organic compound were a hexose-compound, as maintained by HARDEN and YOUNG, fermentation by living yeast should take place after the sugar, a hexose in this case, has been liberated from the phosphate. Since such fermentation does not take place, the sugar liberated must be a triose. Third, since "Hefanol," which by washing has been freed from "synthease," will ferment triose-phosphate but not glucose, the synthesis of the triose-phosphate is a necessary intermediate step in the fermentation of sugar.

The author represents his view of the course of fermentation in three stages: (1) depolymerization of glucose, (2) synthesis of triose-phosphate by the soluble enzyme "synthease," and (3) splitting of the triose-phosphate by "alcoholase," an almost insoluble enzyme remaining in the zymin residue after washing.

In a later paper,[5] somewhat controversial in its nature, HARDEN and YOUNG present the results of further studies bearing directly on IWANOFF's contentions. They point out that if IWANOFF's formulation of the process of fermentation is correct, the triose-phosphate of IWANOFF is an intermediate compound, the formation of which *precedes* the evolution of carbon dioxid; whereas the authors have shown that the formation of the phospho-organic compound is *accompanied* by the evolution of carbon dioxid. The case is the same whether yeast juice or zymin is used. It is further shown that the filtrate from a fermenting mixture of cane sugar and zymin, prepared after the method of IWANOFF, is still capable of producing fermentation; therefore the formation of the phospho-organic compound taking place when phosphates are added to such filtrate, is not proof that the phospho-organic compound can be formed without the accompaniment of fermentation. With regard to IWANOFF'S "synthease," the authors show that the process of washing zymin employed by IWANOFF removes the soluble coenzyme of yeast juice, without which fermentation does not take place. When the boiled washings are added to the residue, the power to ferment glucose is restored. The loss of fermenting power of washed zymin is explained, therefore, by the removal of a soluble thermostable coenzyme. Since the boiled washings, if added to the residue, restore its power of fermentation, the authors contend that the reactivating power is not due to IWANOFF'S "synthease," which therefore has no existence.

Other experiments bearing on this subject have been reported in another paper by HARDEN and YOUNG.[6] Several phases of the question are taken

[5] HARDEN, A., and YOUNG, W. J., The function of phosphates in alcoholic fermentation. Centralbl. Bakt. II. **26**:178–184. 1910.

[6] ——— The alcoholic ferment of yeast juice. Proc. Roy. Soc. B **82**:321–330. 1910.

up individually. The first series of experiments relating to the ratio of carbon dioxid to sugar fermented in the presence of excess of phosphates shows that the ratio agrees with that derived from the reaction formula given by the authors, that is, $2C_6H_{12}O_6 \rightarrow 2CO_2$, for the period of accelerated fermentation that follows the addition of phosphates to a fermenting mixture.

The question as to the necessity of phosphates for alcoholic fermentation is also taken up. While it has never been conclusively shown that alcoholic fermentation cannot take place in the absence of phosphates, the experiments here given furnish strong evidence in favor of the view that phosphates are necessary for alcoholic fermentation. The authors reduced the quantity of phosphates in fermenting mixtures to a minimum, and found that the addition of very small quantities of phosphates to such mixtures increased the evolution of carbon dioxid as much as 700 per cent of the original amount; while if no precaution is taken to remove the phosphates from the mixture at first, further addition of phosphates gives an increase of only 10–150 per cent of the original. The relatively large increase in fermentation due to the addition of small quantities of phosphates is regarded as strong evidence that phosphates are necessary in fermentation.

It is further shown that the hexose-phosphate when hydrolyzed by the enzymes of yeast juice yields a sugar which is fermented by living yeast, a result which is opposed to the conclusion of IWANOFF mentioned above. The sugar thus obtained gives the reactions of fructose, although the possibility that other hexoses may be present is not excluded.

Putting the facts thus far gained into the shape of a tentative theory, HARDEN and YOUNG suggest that two molecules of hexose may be decomposed into smaller groups, two of which go to form alcohol and carbon dioxid. The other two residues are synthesized into a new chain of six carbon atoms, which forms the carbohydrate part of the hexose-phosphate.

Papers taking up the question of fermentation from a different viewpoint have been published by KOHL and by KUSSEROW. KOHL'S[7] work relates chiefly to the part played by the enzymes in the different steps of fermentation. As far as the steps by which sugar is transformed into alcohol are concerned, he adheres to the original view of BUCHNER that lactic acid is an intermediate product. BUCHNER attributes the first step in this process to the action of an enzyme which he called zymase, and which is not easily extracted from the cells by the usual solvents for enzymes. KOHL finds that none of the enzymes extracted from yeast by glycerin or water are capable of transforming lactic acid into alcohol and carbon dioxid. It is therefore this step, he reasons, and not the changing of sugar into lactic acid, which must be attributed to the action of zymase. This leaves the splitting of lactic acid into alcohol and carbon dioxid to be accomplished by some of the soluble enzymes of the yeast

[7] KOHL, F. G., Ueber das Wesen der Alkoholgärung. Beih. Bot. Centralbl. I. 25:115–126. 1910.

extract. It is here that the author finds a function for catalase. The extract is rich in catalase, and since no other function for this enzyme is known, he makes it the active agent in the first step of fermentation according to the scheme. Nor is this view reached without apparent experimental evidence. Extracts of yeast rich in catalase were allowed to act for various lengths of time on 10 per cent glucose solutions. The solutions were found to contain lactic acid, which was identified by its zinc and calcium salts and by other tests. Unfortunately the experiments are not entirely convincing, since the only precaution to insure sterility was the addition of thymol to the flasks. It is not recorded that cultures were made from the flasks at the end of the experiments to demonstrate their sterility. The finding of oxalic acid in the flasks would seem to add to the doubtfulness of the experiments.

KUSSEROW,[8] believing that no description of the mechanism of fermentation has been given, propounds a new theory of alcoholic fermentation. This theory is that the demand of the yeast cell for oxygen results in the reduction of glucose to sorbite, a molecule of water being involved in the reaction. The sorbite breaks up directly into alcohol, carbon dioxid, and hydrogen. The hydrogen reduces a further molecule of glucose, and so the process goes on. The view is scarcely supported by evidence, nor would the dearth of theories alone seem to warrant it, for several have been proposed.—H. HASSELBRING.

Vegetative reproduction in Metzgeria.—EVANS[9] has described the gemmae of 12 species of *Metzgeria*. They fall into three groups, depending upon their position on the thallus. The first group (5 spp.) has the gemmae marginal; the second (6 spp.) has them on the antical surface of the wings; and in the third group (1 sp.) they are indefinite in position. When a gemma is to be produced, a marginal cell projects beyond its neighbors and its outer wall is ruptured. The protruding protoplast is not naked, however, but is covered by a thick layer of transparent gelatinous substance, which EVANS thinks is a modification of the inner portion of the original wall. Upon the inner surface of this gelatinous substance a very thin new wall soon appears. The projecting cell divides by a periclinal wall; the outer of these two cells is considered to be the mother cell of the gemma. A second wall meets the first, obliquely cutting off a wedge-shaped apical cell, which proceeds to cut off segments right and left. The original gelatinous substance becomes stretched by the growth of the gemma until it finally disappears. The gemma is separated from the plant by the splitting of the original periclinal wall. Along the margin of the young gemma hooked hairs appear. As it becomes older, new hairs appear, which function as rhizoids. The young gemma shows no sign of dorsiventrality.

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[8] KUSSEROW, R., Centralbl. Bakt. II. **26**:184–187. 1910.

[9] EVANS, ALEXANDER W., Vegetative reproduction in *Metzgeria*. Annals of Botany **24**:272–303. *figs. 16*. 1910.

EVANS thinks that a vigorous apical cell exercises an inhibitory action on the production of gemmae, and that when the apical cell is suppressed, or its activity lessened, gemmae are able to form. He says:

> Just why the normal activities of the apical region are lessened in these cases and finally brought to an end, is by no means clear. In some instances the result is perhaps due to poor nutrition, bringing about an enfeeblement of the whole plant; but this cannot be the effective cause in all cases, because a limitation of growth often takes place in plants which are robust. Under these circumstances the plant is probably able to control the apical growth, perhaps by diverting the currents of food to other regions. Apparently something of the same sort takes place in such species as *M. dichotoma*, where the growth of the gemmiparous branch continues for an indefinite period. The power of the plant to regulate the distribution of the nutritive materials, and thus to weaken or destroy the inhibitory influence exerted by the apical region upon the cells capable of producing gemmae, may be considered a specific character.

It seems possible that the production of gemmae may rather be due to the influence of some external factor than to an internal self-regulating mechanism; and it is possible by experiment to determine what this factor may be.—W. J. G. LAND.

Presentation time.—RUTGERS,[10] working in WENT'S laboratory at Utrecht, has studied the relation of temperature to geotropic presentation time in the etiolated seedlings of *Avena*. He believes that VAN'T HOFF'S law of speed of reaction for temperature holds from 5° to 30° C. with a coefficient of about 2.6 for every rise of 10°. From 0° to 10° the coefficient is 6.8. RUTGERS attributes this high coefficient to the effect of low temperature on growth. From 25° to 35° the coefficient is 0.93, and for higher temperatures still lower. The time of previous warming (varying 1 to 24 hours) has no effect up to 25°; but at 30° its effect is marked. At the latter temperature one hour's warming gives a presentation time of 3.5 min.; while 12 to 24 hours gives 1.66 minutes. These results do not agree with those of BACH.[11] It is certainly interesting, if true, that this chemical law applies to this supposedly complex process of perception as BLACKMAN[12] has shown it to apply in photosynthesis, and KUYPER[13] in respiration, and various other workers in other processes.

Serious criticism can be offered against RUTGERS' methods and his discussion of literature. So far as his description of methods tells, he seems to

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[10] RUTGERS, A. A. L., The influence of temperature on the presentation time in geotropism. English reprint from the Proc. Konink. Akad. Wetensch. Amsterdam. Oct. 29, 1910.

[11] Bach, H., Ueber die Abhängigkeit der geotropischen Präsentation und Reaktionzeit von verschiedenen Aussenbedingungen. Jahrb. Wiss. Bot. **44**:57–123. 1907.

[12] BLACKMAN, F. F., Optima and limiting factors. Annals of Botany **19**:281–295. 1905.

[13] BOT. GAZETTE **50**:233–234. 1910.

have depended upon the unaided eye to detect reaction, and the work was done without the use of a clinostat. Methods of such crudeness must give questionable data. He states that BACH'S results are not suited to test VAN'T HOFF'S law, but so far as they give data they indicate a coefficient of 3.75. In contrast to this statement it should be mentioned that BACH determined the presentation time in the epicotyl of *Vicia Faba* for every two-degree change from 14° to 34°. This was done by accurate methods, and one must conclude that Bach's figures are good for testing the application of the VAN'T HOFF law between 14° and 34°. The following are the coefficients figured from BACH'S table: 14°–24°, 3.88; 16°–26°, 4.61; 18°–28°, 4.54; 20°–30°, 3.80; 22°–32°, 2.00; 24°–34°, 1.59. As is seen here, the coefficient is rather variable.—WILLIAM CROCKER.

Anatomy of Welwitschia.—Miss SYKES[14] has investigated a large number of seedlings and young plants of *Welwitschia*, placed at her disposal by Professor PEARSON. The mature plant is aptly spoken of as an "adult seedling," since the main axis consists of root and much enlarged hypocotyl. Two ridges are developed by rapidly dividing parenchyma, the inner one bearing the strobiliferous axes. Each cotyledon is supplied by a pair of collateral bundles, which unite to form one pole of the diarch root, the transition being remarkably slow, probably on account of the great length of the hypocotyl. The four cotyledonary bundles are joined by the bundles from the buds, ridges, and leaves; this association of bundles forming four concentric groups, so that there is at no time any real stem structure. In the character of four cotyledonary bundles connected with a diarch root, *Welwitschia* is associated with *Araucaria* and *Podocarpus*, and also in the details of the transition. The small amount of primary vascular tissue is a remarkable feature, being limited to the root poles, the four cotyledonary bundles, and the four connecting hypocotyledonary bundles. In the base of the cotyledon, centripetal xylem is developed in connection with the two bundles, and of course the bundles traversing the hypocotyl become exarch.

The retention of the seedling characters in the adult plant makes a comparison impossible with the stem structure of other groups; and if the vascular structure of seedlings depends to a large extent upon "habitat and environment," as the author considers probable, a seedling comparison cannot be significant in indicating relationships. The result of the study, therefore, has been to uncover some interesting facts in reference to the anatomy of *Welwitschia*, rather than to uncover some much needed suggestion as to relationship.—J. M. C.

[14] SYKES, M. G., The anatomy of *Welwitschia mirabilis* in the seedling and adult states. Trans. Linn. Soc. London II. Bot. **7**:327–354. *pls. 34, 35. figs. 5.* 1910.

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